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CONTENTS

A REVISION OF THE NORTH AMERICAN BUPRESTID BEETLES BELONGING TO THE GENUS MELANOPHILA

(COLEOPTERA, BUPRESTIDAE)

BY

KENNETH D. SLOOP

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INTRODUCTION

THIS PAPER represents an attempt to present a revision of the North American Buprestid beetles of the genus *Melanophila*. The latest revision of this genus being that of Dr. George H. Horn (1882), and the students of Buprestidae having long considered the genus a somewhat heterogeneous group, it seems advisable to assemble the more recent information and give keys and, as far as possible, other data of importance. An attempt will be made to interpret the generic relationship of the various species based on structure and biology. Because many of the species of this genus are among the most important insect pests of the forest, attention will be given to the economic importance of each species.

ACKNOWLEDGMENTS

THE GENUS: ITS SYSTEMATIC POSITION

The genus *Melanophila*, as it has been known, belongs to the group Anthaxiae of the tribe Buprestini (Horn, 1882). The group Anthaxiae in North America is composed of three genera: *Anthaxia, Xenorhipis,* and *Melanophila.*

DISTRIBUTION

Members of the genus *Melanophila* are found throughout North America, eighteen species being recorded from the United States and Canada. Three species are found in Mexico and one species with one variety in Central America. There are also a number of species recorded from Europe and Asia.

In North America the species of this genus are found to be most abundant in the southern part of the United States. All the eighteen species known from North America are found in this region and seven species are found nowhere else.

According to Obenberger, 1928, *M. acuminata* is the only species found in the entire holarctic region as well as in part of the nearctic regions.

BIOLOGY

The various species of *Melanophila* breed principally in coniferous trees, although the author has collected *M. occidentalis* Obenberger under the bark of burned oak and one specimen of *M. consputa* LeConte in southern California in the larval channel under the bark of *Eucalyptus globulus* Labill.

The adults are, as a rule, collected by beating the terminal twigs of the various conifers or taken from the bark of dead or weakened trees. They are also easily reared from the bark where they pupate.

The members of a species are somewhat gregarious, as is shown by the fact that trees possessing no other insects in the bark except secondary entrants are often found in the forest. These trees are called by the forest entomologists "flathead" trees.

One of the most peculiar biological reactions among Coleoptera is exhibited by a few of the members of this genus, namely, swarming to fires giving off an acrid smoke. Dr. E. C. Van Dyke, 1926, reported the capture of large numbers of *Melanophila consputa* Lec. that were found to be swarming about a large oil fire at Coalinga, California. Coalinga is between fifty and one hundred miles from any coniferous forests, indicating that these insects were able to detect the smoke and fly to it over long distances. Dr. Van Dyke, 1928, also reported the swarming of *M. consputa* Lec. about the vats containing the hot sugar syrup in the Western Sugar Refinery in San Francisco. The authorities of the refinery said that the swarming of this insect was a common occurrence in the late summer and fall. Mr. E. G. Linsley, 1933, reported the swarming of *M. consputa* Lec. and *M. atropurpurea* Say to brush and grass fires in the hills behind Oakland. He also states that in June, 1932, large numbers of *Melanophila* were collected about the street lights of Douglas, Arizona—attracted, possibly, by the acrid fumes of the large smelter plant in that city. The species represented were *M. consputa* Lec. and *M. acuminata* De Geer, with *acuminata* in preponderance. Two specimens of a variety of *M. notata* Castelnau, new to science, were also taken. The habit, common to several species, of swarming about burning sawdust and slash near lumber mills is in fact so well known to lumbermen that these beetles have long been known as "fire bugs."

As Mr. Linsley, 1933, points out, all the species found swarming to fires are of the *acuminata* type, none of the *gentilis* group having been found to react in this manner to smoke.

CHARACTERS USED IN CLASSIFICATION

The members of the genus *Melanophila* may be readily separated into several distinct units on the basis of general facies. The separation of the species is, however, often extremely difficult. A search for additional morphological characters, upon which to base the separation of the various units of species, has disclosed some interesting facts. These characters may be discussed briefly as follows.

Head.—Obenberger, 1928, says that the form and sculpture of the vertex and clypeus are useful in the separation of the species of *Melanophila.*

Thorax.—The shape and sculpture of the pronotum are often valuable in separating species of a unit from each other. A study of the ventral surface of the thoracic segments disclosed a sensory pit, contiguous with the lateral margin of the coxal cavity of the middle pair of legs. This structure is found on all the species of the *acuminata* or flattened type (i.e.: *M. consputa* Lec., *M. notata* Cast. et Gory, *M. opaca* Lec., *M. atropurpurea* Say, and *M. acuminata* De G.). This sensory pit is found in none of the species of the *gentilis* type. It is of interest to note that all the species possessing this sensory pit are the species that fly to fire.

Elytra.—The elytra are of some value in separating the various species; the apices may be truncate or acute and the sculpturing is often different enough to be of taxonomic value.

Wings.—The wings show an interesting difference of taxonomic value. In the *acuminata* group the anal veins are nonpigmented, whereas in the species belonging to the *gentilis* type all the veins are well pigmented. In a few individuals of the *gentilis* group the lower veins are not so heavily pigmented, but as a unit they are always heavier by far than they are in the members of the *acuminata* group.

Legs.—The comparative lengths of the various parts of the legs and tarsi often help in differentiating the species of this genus.

Genitalia.—This study indicates that the genitalia show good usable differences (which will be discussed more fully later). The comparative length of the aedeagus to the side pieces is here considered of no value, because there is a distinct membrane at the base of this part which would make possible a certain amount of protrusibility.

THE GROUP ANTHAXIAE LeCONTE AND HORN

The genus *Melanophila* is, as has been previously stated, a somewhat heterogeneous group. Dr. Horn, 1882, recognized three types indicated by external form and general aspect: first, the *Chrysobothris* type, represented by *drummondi;* second, the Anthaxiae, represented by *notata, miranda, atropurpurea, acuminata,* and *consputa;* and finally, a group of five species that do not resemble any other genus in our fauna.

Obenberger, 1928, recognizes two groups of the *Melanophila* in North America. One group corresponds to the true *Melanophila,* the typical representative of which is *acuminata;* the second group is closely related to the European genus *Phaenops.* This division is applicable to the species of Europe as well as to those of North America.

In Europe the genus *Phaenops* is recognized for three species: *cyanea, aerea,* and *knoteki.* It is of importance to note that *cyanea* is very closely related to the North American species, *gentilis,* in its color, general facies, and morphological characters.

It is the author's opinion that the two groups of *Melanophila* previously

mentioned constitute individual homogeneous units. Since both forms occur throughout the entire holarctic region, the separation of the two types must have been early indeed. Therefore, considering the biological importance of the sensory pits on the ventral surface of the mesothorax with respect to the reactions of the *acuminata* group, and the generic importance of this character when it is combined with the absence of pigmentation in the veins of the lower part of the wings and the general facies, it seems logical to separate these two groups, placing the *gentilis* group in the European subgenus *Phaenops* and the *acuminata* group in the genus *Melanophila*.

Melanophila miranda Lec. is somewhat difficult to place, because it has the general facies of *acuminata* but lacks the sensory pits of the mesothorax, and the anal veins of the wings are slightly pigmented at the base. This species is the only one in North America to have smooth, raised callosities on the head and prothorax. It thus represents a unit in itself and will be placed as a separate subgenus.

The following table, modified from Horn, 1882, separates the genera of the group Anthaxiae.

KEY TO THE GENERA OF THE GROUP ANTHAXIAE

1. Mentum corneous in front, prothorax sinuate at base........................... 2
   Mentum entirely corneous.. 4
2. Flattened, head and thorax without smooth facets, a distinct pit contiguous to the lateral margin of the middle coxal cavity............................*Melanophila* (S. str.)
   More or less convex; no pits contiguous to lateral margin of middle coxal cavities.... 3
3. Apices of elytra not acute, head and thorax without large smooth facets..............
   Melanophila subgen. *Phaenops*
   Apices of elytra acute, head and thorax with smooth facets.........................
   Melanophila subgen. *Xenomelanophila*
4. Prothorax truncate at base; front not margined at sides; antennae serrate in both sexes..
   Anthaxia
   Prothorax sinuate at base; front slightly margined over the insertion of the antennae, which are flabellate in the male and serrate in the female................*Xenorhipis*

Genus MELANOPHILA Eschscholtz

Melanophila Eschscholtz, 1829, Zool. Atlas, p. 9.
Melanophila Lacordaire, 1837, Gén. Coléop., IV:47.
Melanophila LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:211.
Melanophila LeConte, 1861 (Smithsonian Misc. Coll.), p. 153.
Melanophila Marseul, 1865, L'Abeille, II:193.
Melanophila Horn, 1882, Trans. Am. Entom. Soc., X:1.
Melanophila Waterhouse, 1887, Biol. Centr.-Am. Coleop., III, 1st ser., pp. 16, 176, 663.
Melanophila Fisher, 1925, Proc. U. S. Nat. Mus., 65:170.

Subgenus MELANOPHILA Eschscholtz

Flattened dorsoventrally, black, shining, occasionally marked with yellow. Head about as broad as long, front punctured, antennae serrate, often reaching hind angles of prothorax. Prothorax broader than long. Mesothorax with two small sensory pits contiguous
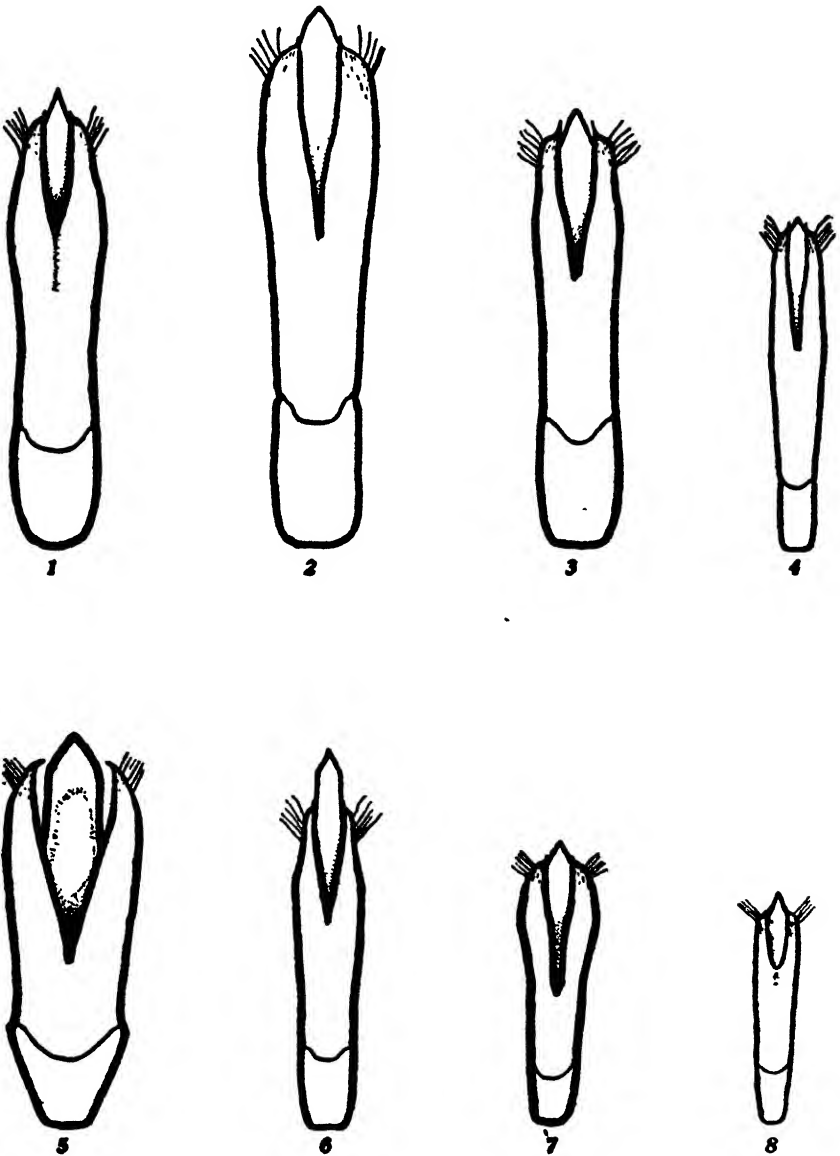
All the genitalia are enlarged in the same proportion except *fulvoguttata* and *pini-edulis*, which are slightly more enlarged than the others.

Fig. 1. Male genitalia of *M. gentilis* LeConte
Fig. 2. Male genitalia of *M. fulvoguttata* (Harris)
Fig. 3. Male genitalia of *M. pini-edulis* Burke
Fig. 4. Male genitalia of *M. californica* Van Dyke
Fig. 5. Male genitalia of *M. miranda* LeConte
Fig. 6. Male genitalia of *M. drummondi* Kirby
Fig. 7. Male genitalia of *M. intrusa* Horn
Fig. 8. Male genitalia of *M. aeneola* Mels.

to lateral margin of the middle coxal cavities. Elytra usually acute at apex, occasionally with a sharp apical spine. Wings with anal veins not pigmented, the other veins normal. Legs black, slightly punctured and clothed with short recumbent hairs. Apices of the side pieces of the male genitalia not produced into a short spine parallel to the aedeagus.

Genotype *Melanophila acuminata* De Geer

This subgenus is readily separated from the other subgenera of *Melanophila* by the pits on the mesosternum. The North American species that belong to this subgenus may be separated by the following table.

KEY TO NORTH AMERICAN SPECIES OF SUBGENUS
MELANOPHILA ESCH.

1. Black with yellow markings... 2
   Black without yellow markings... 5
2. Elytral markings in the form of spots... 3
   Elytral markings not in the form of spots..................................... 4
3. Last segment of tarsi almost as long as first, front densely punctured, elytra with two to twelve yellow spots, body beneath bronze. Western states..............(1) *consputa*
   Last segment of tarsi distinctly shorter than first, front sparsely punctured, elytra with six to eight yellow spots, body beneath blue-green. Georgia and Florida......(2) *notata*
4. Yellow markings forming an inverted block A.
   Last tarsal segment shorter than first, third and fourth antennal segments subequal in length. Arizona...*notata* subsp. *elegans*
5. Elytra acute at apex... 6
   Elytra acuminate at apex... 7
6. Front sparsely punctured, legs blue-black, disk of thorax deeply, granulately punctate. Florida and Georgia...(4) *opaca*
   Front equally densely punctate; legs bronze; disk of thorax smooth, shallowly granulately punctate. Entire holarctic region............................(5) *acuminata*
7. Legs bronze, front closely, coarsely punctate; prothorax widest in front of middle, rough, reticulate-punctate; disk of elytra roughly granulately punctate. California...........
                                                                    (6) *occidentalis*
   Legs blue-green, front closely, very finely punctate; prothorax widest at middle, smooth, slightly granulately punctate; disk of elytra smoothly granulately punctate. Arizona, Texas, Utah...(7) *atropurpurea*

(1) *Melanophila consputa* LeConte

Melanophila consputa LeConte, 1857, Rep. Pac. Explor., XII:44.
Melanophila consputa LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:212.
Melanophila consputa Horn, 1882, Trans. Am. Entom. Soc., X:103.
Melanophila consputa Kerr, 1905, Mem. Soc. Entom. Belg. Bupr., XII:106.
Melanophila consputa ab. *monochroa* Obenberger, 1928, Archiv. Naturg., Bd. XCII, Abt. A, p. 209.
Melanophila consputa ab. *isolata* Obenberger, *ibid.*

Flattened dorsoventrally, black with yellow spots. Front equally densely punctured, shining, glabrous; antennae just reaching hind angles of prothorax; third segment slightly longer than second. Pronotum granulate-punctate, shining, lateral margins visible only at base when viewed from above, widest in front of middle, disk with a median longitudinal depression, often vaguely indicated. Elytra broadest near apex, granulate-punctate, non-

costate, subobtuse at apex, ten to twelve yellow spots forming a pattern. Body beneath black, shining, sparsely punctured, clothed with short white hairs. Legs black, shining, sparsely punctate, clothed with short recumbent white hairs; first, second, and third tarsal segments padded. Average length 11 mm., width 4 mm.

Distribution.—California, Arizona.

Host plants.—Yellow pine (*Pinus ponderosa*), Eucalyptus sp., lodgepole pine (*P. murrayana*), Monterey pine (*P. radiata*), and knobcone pine (*P. attenuata*).

This species is readily separated from *notata*, the only other species having yellow spots on the elytra, by the generally larger size, less shining head and thorax, and more finely punctured pronotum. *M. consputa* usually has ten or twelve spots on the elytra, and *notata* has six or eight.

(2) *Melanophila notata* (Castelnau)

Aptura notata Castelnau et Gory, 1837, Monogr. Bupr., I:4.
Melanophila notata Lacordaire, 1857, Gén. Coléop., IV:48.
Melanophila notata LeConte, 1857, Proc. Acad. Nat. Sci. Phila., IX:7.
Melanophila notata LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:212.
Melanophila notata Horn, 1882, Trans. Am. Entom. Soc., X:103.
Melanophila notata Fisher, 1925, Proc. U. S. Nat. Mus., LXV:171.
Melanophila leuteosignata Mannerheim, 1837, Bull. Soc. Imp. Nat. Moscow, X:70.
Phaeonops leuteosignata Ziegler, 1845, Proc. Acad. Nat. Sci. Phila., II:267.

Flattened, black with six to eight yellow spots. Front rather sparsely, coarsely punctate; antennae blue-green, third segment subequal to fourth. Disk of thorax granulately punctate, somewhat rough; sides rounded from base to apex, widest slightly in front of middle. Elytral apices acute, not prolonged; disk deeply, closely granulately punctate; legs and body beneath bronze; sparsely clothed with short recumbent white hairs. Length 10 mm., width 4 mm.

Distribution.—Florida, Georgia, middle and southern states, Cuba, and Mexico.
Host plants.—Unknown.

This species is readily separated from *consputa* as previously mentioned. It is separated from the species which follow by the bronze legs, more irregular pronotum, and the elytral markings.

(3) *Melanophila notata* subsp. *elegans* Sloop, n. subsp.

Black with yellow markings on the elytra. Head closely, rather coarsely punctate; antennae blue-green, extending to slightly beyond hind angles; pronotum smoothly reticulate-punctate at sides, granulate-punctate on disk, sides evenly rounded from base to apex, widest slightly in front of middle. Elytra acute at apex, sides almost parallel for first two-thirds, thence suddenly narrowing to apex; disk smoothly granulately punctate, yellow markings forming an inverted block A. Body beneath black; legs blue, moderately clothed with rather long white pile. Length 10 mm., width 4 mm.

Distribution.—Arizona.
Host plant.—Unknown.

Holotype, female (no. 4537, Mus. Calif. Acad. Sci.), and one paratype in the collection of the author, taken at Douglas, Arizona, on June 7, 1932, by Mr. E. Gorton Linsley, who kindly presented the specimens to me for study.

This subspecies is closely related to *M. notata* but may be readily separated from the typical species by the yellow inverted block A on the elytra and the smoother and more robust prothorax.

(4) *Melanophila opaca* LeConte

Melanophila opaca LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:213.
Melanophila notata Crotch, 1873, Proc. Acad. Nat. Sci. Phila., XXV:89.

Black, robust, subopaque. Front somewhat sparsely, deeply punctate; antennae blue-green, shining, just reaching hind angles of prothorax; third segment distinctly longer than second and about as long as fourth. Pronotum finely granulately punctate; sides evenly rounded from base to apex, as wide at base as at apex, widest in front of middle. Elytra acute at apex, evenly, coarsely granulately punctate; widest at humeral angles. Body beneath bronzy black; legs somewhat blue-green, clothed with short white pile. Length 11 mm., width 4 mm.

Distribution.—Georgia and Florida.
Host plant.—Unknown.

This species is probably most closely related to *notata*, but lacks the yellow spots of that species. It may be separated from *acuminata* by the more sparsely punctured front and rougher disk of the thorax.

(5) *Melanophila acuminata* De Geer

Buprestis acuminata De Geer, 1774, Mem. Hist. Ins., IV:133.
Melanophila acuminata Eschscholtz, 1829, Zool. Atlas, p. 9.
Melanophila acuminata Fisher, 1925, Proc. U. S. Nat. Mus., LXV:173.
Melanophila acuminata Obenberger, 1926, Archiv Naturg., Bd. XCII, Abt. A, p. 209.
Buprestis acuta Gmelin, 1778, Lin. Syst. Nat., 13th ed., Vol. I, Pt. IV, p. 1939.
Buprestis morio Fabricius, 1792, Ent. Syst., Vol. I, Pt. II, pp. 210–211.
Buprestis appendiculata Fabricius, 1792, *ibid.*, p. 210.
Phaenops appendiculata Dejean, 1836, Cat. Coleop., 3d ed., p. 89.
Oxypteris appendiculata Kirby, 1837, Richardson's Fauna Bor.-Am., IV:160.
Apatura appendiculata Castelnau et Gory, 1837, Monogr. Bupr., I, Apatura, p. 8, table 2, fig. 14.
Anthaxia pecchiolii Castelnau et Gory, 1837, Monogr. Bupr., II, Apatura, p. 33.
Buprestis longipes Say, 1823, Jour. Acad. Nat. Sci. Phila., III:164.
Melanophila longipes Mannerheim, 1837, Bull. Soc. Imp. Nat. Moscow, X:70.
Melanophila longipes LeConte, 1857, Trans. Am. Philos. Soc. (2), XI:212.
Melanophila immaculata Mannerheim, 1837, Bull. Soc. Imp. Nat. Moscow, X:70.

Black, feebly shining, front densely punctured; antennae extending to slightly beyond hind angles of prothorax, third segment almost twice as long as second. Thorax coarsely punctured along the margin, obsoletely, granulately punctate on disk, which is almost smooth; median longitudinal depression distinct at base and apex. Elytra moderately finely granulately punctate, the surface irregular, lateral margin finely serrate near apex, apices acute but not acuminate. Body beneath black, feebly shining, moderately clothed with short white hairs. Length 10 mm., width 4 mm.

Distribution.—The more northern part of the entire holarctic region.
Host plants.—Many pines, firs, and spruces.

Melanophila acuminata can be separated from *atropurpurea* and *occidentalis* by the acute apices of the elytra. In *acuminata* the front is densely punctured; in *atropurpurea* the head is somewhat sparsely punctured. In *acuminata* the prothorax is widest in front of the middle; in *atropurpurea* it is widest at middle. The genitalia of these three species show striking differences, as shown in the plates. A study of the genitalia seems to indicate beyond question that *M. atropurpurea* Say is distinct from *M. acuminata* De G.
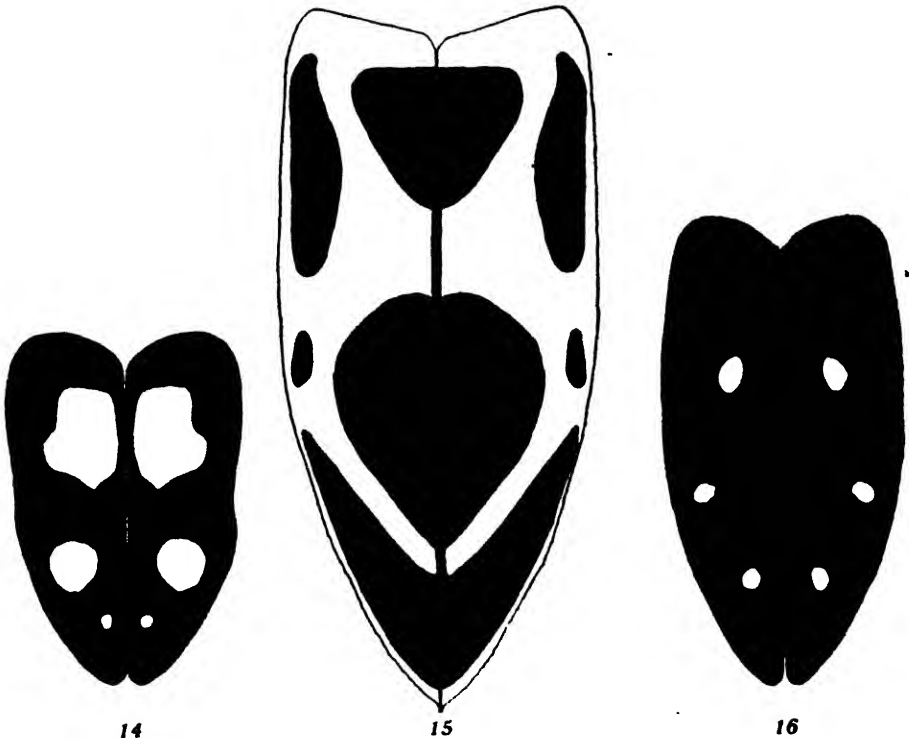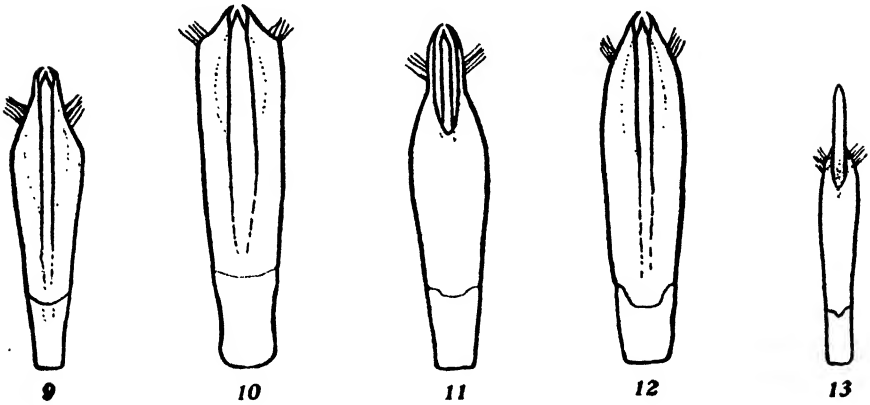
Fig. 9. Male genitalia of *M. acuminata* De Geer
Fig. 10. Male genitalia of *M. atropurpurea* Say
Fig. 11. Male genitalia of *M. consputa* LeConte
Fig. 12. Male genitalia of *M. occidentalis* Obenberger
Fig. 13. Male genitalia of *M. aeneola* Mels.
Fig. 14. Elytra of *M. pini-edulis* Burke
Fig. 15. Elytra of *M. miranda* LeConte
Fig. 16. Elytra of *M. drummondi* Kirby

Fig. 13 is a second drawing of male genitalia of *M. aencola* Mels. to show the variation that may occur within a species.

(6) *Melanophila occidentalis* Obenberger

Melanophila occidentalis Obenberger, 1928, Archiv Naturg., Bd. XCII, Abt. A, p. 209.

Flattened, black, shining. Front sparsely, coarsely punctured; antennae reaching hind angles of prothorax, second segment only slightly longer than fourth, distinctly longer than second. Pronotum granulate-punctate on disk, becoming reticulate at margins, usually widest in front of middle. Elytra granulate-punctate, sides almost parallel for basal two-thirds, thence suddenly converging to apex, which is acuminate. Body beneath bronze and shining, clothed with short white hairs; legs bronze, first segment of hind tarsi distinctly longer than following two. Length 10 mm., width 3.5 mm.

Distribution.—California.

Host plant.—A series of fifty specimens taken from under the bark of a burned oak in Orange Co., Calif.

This species may be best separated from *acuminata* and *atropurpurea* by reference to the genitalia. The front is less densely punctured and the disk of the pronotum and elytra are more evenly granulate-punctate. The thorax is widest in front of middle and the apices of the elytra are acuminate.

(7) *Melanophila atropurpurea* Say

Melanophila atropurpurea Say, 1836, Trans. Am. Philos. Soc. (2), XI:213.
Melanophila atropurpurea Horn, 1882, Trans. Am. Entom. Soc., X:104.
Melanophila atropurpurea Hamilton, 1894, Trans. Am. Entom. Soc., XXI:29.
Melanophila atropurpurea Nicolay, 1921, Jour. New York Entom. Soc., XXIX:174.
Melanophila atropurpurea Obenberger, 1928, Archiv Naturg., Bd. XCII, Abt. A, p. 208.

Black, robust, feebly shining. Front finely, densely punctured; clypeus arcuately emarginate at middle; antennae shining, blue-green, third segment longer than second and fourth. Pronotum reticulate-punctate only at margins, entire disk finely, smoothly, granulate-punctate; sides evenly rounded from base to apex, widest at middle, anterior one-third of lateral margin obliterated. Prothorax beneath finely, densely punctate. Elytra finely, smoothly, granulate-punctate; sides subparallel, widest at base and apical two-thirds, acuminate at apex. Body beneath black, shining; legs blue-green, shining, sparsely clothed with short white pile. Lateral margins of the side pieces of male genitalia diverging slightly from base for seven-eighths the distance to apex, thence suddenly converging to apex, widest very near apex. Average length 7 mm., width 3 mm.

Distribution.—Arizona, Texas, Utah, Arkansas (Say).

Host plant.—*P. ponderosa*, Douglas fir, and true firs.

M. atropurpurea is probably closely related to *M. acuminata*, but may readily be separated from that species by the general facies of the genitalia. In *acuminata* the genitalia are widest two-thirds from base, and in *atropurpurea* the widest point is one-eighth from apex, whereas in *occidentalis* the sides are evenly rounded from base to apex with no sudden converging as in the two previously mentioned species.

Subgenus PHAENOPS Lacordaire

Phaenops Lacordaire, 1857, Gén. Coléop., IV:47.

Robust, convex, black or green, often with yellow spots on the elytra. Front punctured, never with callosities; antennae serrate from third or fourth segments. Prothorax punctate on disk, margins visible only at base when viewed from above. Mesothorax without sensory pits contiguous to lateral margins of middle coxal cavities. Elytra punctate, occasionally

costate, in some species pubescent, margins parallel or diverging to widest point two-thirds from base; body beneath shining, usually green. Wings with lower veins well pigmented.

Genotype *Buprestis cyanea* Fabricius

The North American species belonging to this subgenus have previously all been placed in the genus *Melanophila.* At the present time, however, good characters are known upon which to separate into two groups the species of the old genus *Melanophila* and so place them that they will be in their proper phylogenetic position. All the species placed in this subgenus have no sensory pit contiguous to the coxal cavities of the middle pair of legs. They do not fly to fires, as do the true *Melanophila,* indicating that this pit is olfactory in function in the true *Melanophila.* The lower wing veins of *Phaenops* are more heavily pigmented than in the true *Melanophila,* and since the well-known *Melanophila gentilis* LeC. is closely related to the European species *Phaenops cyanea* F., our North American species congeneric with *gentilis* should all be placed in the subgenus *Phaenops.* The following key will help to separate the North American species of *Phaenops.*

KEY TO THE SPECIES OF THE SUBGENUS PHAENOPS LAC.

1. Subcylindrical, usually not more than 7 mm. in length............................ 1
   Flattened, more robust, more than 7 mm. in length............................. 5
2. Color metallic greenish blue. Georgia...................................(1) *obtusa*
   Color bronze or black... 3
3. Elytra densely pilose, 8–9 mm. long....................................(2) *intrusa*
   Elytra sparsely pilose, pile short, usually less than 8 mm. long.................. 4
4. Elytra finely rugulose-punctate, prothorax widest slightly behind middle. Eastern and southern states..(3) *aeneola*
   Elytra coarsely, closely, deeply punctate; prothorax widest at base. North Carolina....
   (4) *carolina*
5. Color bright green-blue.. 6
   Color bronze or black.. 7
6. Elytra with six yellow spots, disk of pronotum transversely strigose, first tarsal segment of hind legs distinctly longer than second, smaller species 8 mm. New Brunswick.......
   (5) *drummondi* var. *abietes*
   Elytra without maculation, pronotum evenly coarsely, closely, punctate; first segment of hind tarsi about equal to second in length, larger species 11 mm. Northern part of entire United States and southern part of Canada.....................(6) *gentilis*
7. Elytra not costate.. 8
   Elytra feebly costate...10
8. Spots on elytra large, the yellow color covering nearly one-half the surface area.......
   (7) *pini-edulis*
   Spots usually very small, the yellow color covering about one-fifth the surface area... 9
9. Disk of prothorax rough, somewhat strigosely punctate, broad, sides of prothorax arcuate. Eastern United States and Canada..........................(8) *fulvoguttata*
   Disk of prothorax smooth, moderately closely, coarsely, punctate, more linear and convex, sides of prothorax only vaguely arcuate. California...............(9) *californica*
10. Disk of prothorax strigosely punctate, less narrowed at base. Western states.........
    (10) *drummondi*
    Disk of prothorax not strigosely punctate, more narrowed at base. Arizona. (11) *arcuata*

(1) *Melanophila (Phaenops) obtusa* Horn

Melanophila obtusa Horn, 1882, Trans. Am. Entom. Soc., X:106.

"Sub-cylindrical, moderately robust, metallic greenish-blue, elytra darker. Front broad, coarsely but not deeply punctured; clypeus feebly emarginate at middle. Thorax convex, narrowed in front, sides moderately arcuate, margin obliterated in front, surface coarsely, deeply and rather densely punctured; slightly reticulate at the sides, beneath coarsely, deeply and densely punctured; prosternum broadly triangular at tip. Elytra very coarsely punctured at base, becoming granulate posteriorly, the posterior margin finely serrulate, the tips separately rounded. Body beneath coarsely but not densely punctured. Posterior tarsi as in *gentilis*. Length 0.22 inch, width 5.5 mm."

Distribution.—Georgia.

Host plant.—Unknown.

No specimens of this species have been available for study, the foregoing description being a copy of Dr. Horn's 1882 description of the species. The remarks given after the description follow:

"The last ventral segment is slightly truncate and the margin reflexed. I have seen but one specimen of this species which resembles in its form one of the smaller species of *Acmaeodera*. It is more obtuse at either end and more cylindrical than any species in our fauna."

(2) *Melanophila (Phaenops) intrusa* Horn

Melanophila intrusa Horn, 1882, Trans. Am. Entom. Soc., X:105.

Elongate, bronze-gray above. Front rather finely, closely punctate; clypeus broadly, shallowly emarginate; antennae not reaching hind angles of prothorax, third segment longer than second and distinctly longer than fourth. Prothorax widest at middle, sides slightly arcuate from base to apex, margin obliterated anteriorly, disk somewhat coarsely punctate. Elytra densely pilose; smoothly, closely, slightly granulate-punctate, margins slightly serrate at the apices, which are obtuse. Body beneath densely clothed with moderately long white pile, closely punctate. First tarsal segment distinctly longer than second.

Distribution.—Pacific Slope.

Host plants.—(*Pinus lambertiana*), (*P. ponderosa*), (*P. scopulorum*), and (*P. attenuata*).

This species may be separated from *carolina* and *aeneola*, to which it seems to be most closely related, by the larger size, the very pilose elytra, the more pilose undersurfaces, and the more elongate first tarsal segment of the hind legs.

(3) *Melanophila (Phaenops) aeneola* Melsheimer

Melanophila aeneola Melsheimer, 1846, Proc. Acad. Nat. Sci. Phila., II:146.

Melanophila aeneola LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:214.

Melanophila aeneola Horn, 1882, Trans. Am. Entom. Soc., X:106.

Melanophila aeneola Blatchley, 1909, Coleop. of Indiana, p. 786.

Melanophila aeneola Knull, 1922, Canadian Entom., LIV:82.

Melanophila metallica Melsheimer, 1846, Proc. Acad. Nat. Sci. Phila., II:146.

Subcylindrical, prothorax greenish bronze, elytra black. Front densely, finely punctate; clypeus only slightly emarginate, subtruncate; antennae short, not reaching hind angles of prothorax, third segment about twice as long as second or fourth. Disk of pronotum closely, moderately coarsely punctate; widest at base, margin obliterated in front. Disk of elytra closely, feebly, shallowly punctate; somewhat scabrous, densely clothed with short white hairs; margins arcuate. Body beneath green, finely, shallowly punctate; legs bronze. Length 6 mm., width 2 mm.
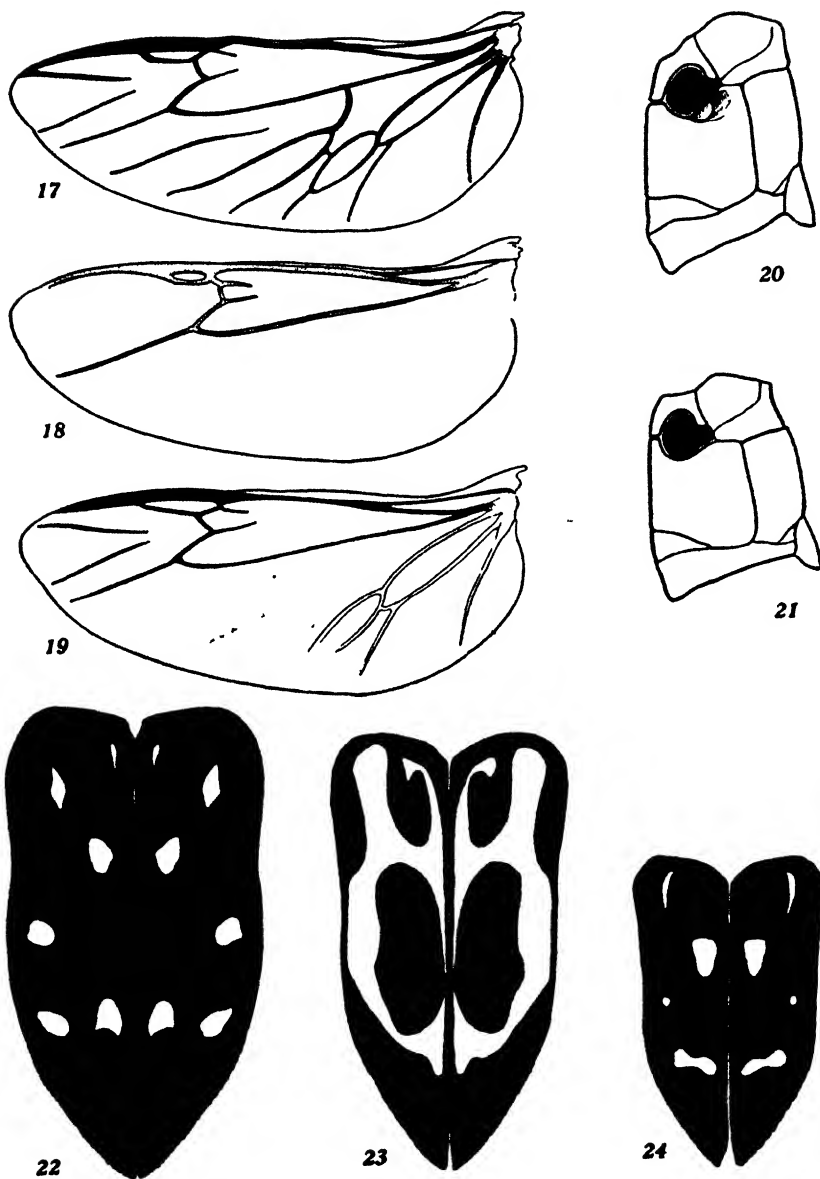
Fig. 17. Wing of *M. gentilis* LeConte
Fig. 18. Wing of *M. acuminata* De Geer
Fig. 19. Wing of *M. (Xenomelanophila) miranda* LeConte
Fig. 20. Ventral view of meso- and metathorax of
                  M. acuminata De Geer
Fig. 21. Ventral view of meso- and metathorax of
                  M. (Phaenops) gentilis LeConte
Fig. 22. Elytra of *M. consputa* LeConte
Fig. 23. Elytra of *M. notata* var. *elegans* Sloop
Fig. 24. Elytra of *M. notata* Castelnau

Figures 17–21 made by Mrs. Frieda Abernathy

Distribution.—Eastern seaboard states, middle and southern states.
Host plants.—*Pinus virginiana* and other pines.

This species may be separated from *obtusa* by the black color and from *carolina* by the less coarsely sculptured prothorax and elytra, and obtuse apices of the side pieces of the male genitalia.

(4) *Melanophila (Phaenops) carolina* Manee

Melanophila carolina Manee, 1913, Entom. News, XXIV:164.

Form subcylindrical, black and somewhat shining. Front coarsely, somewhat closely punctate, clypeus narrow, not produced beneath antennae, very shallowly emarginate; antennae about reaching hind angles, outer segments not strongly serrate, third segment longer than second and fourth. Prothorax closely, coarsely punctate, sides only slightly rounded to the hind angles, which are obtuse. Elytra closely, coarsely punctate, apices obtuse. Body beneath green, shining, sparsely, deeply punctate and clothed with short white pile. Tarsi of hind legs short, first but little longer than second.

Distribution.—North Carolina.
Host plant.—Unknown.

M. carolina is readily separated from *aeneola* by the much coarser punctation of the prothorax and elytra, and the obtuse hind angles of the former. This species has always been rare in collections.

(5) *Melanophila (Phaenops) drummondi* var. *abies* Champlain and Knull

Melanophila drummondi abies Champlain and Knull, 1923, Canadian Entom., LV:105.
Melanophila abietis Obenberger, 1930, Cat. Coleop., Pars III, p. 441.

Broad, robust, green. Front densely, moderately coarsely punctate; antennae about reaching hind angles, third segment twice as long as second and slightly longer than fourth. Prothorax transversely strigose-punctate on disk, coarsely, closely punctate at sides; widest in front of middle; margins obliterated in front. Elytra roughly, coarsely punctate; three vague costae near apices; three small yellow spots on disk; apices obtuse. Body beneath green; smoothly, sparsely, shallowly punctate. First tarsal segment of hind legs only slightly longer than following segment. Length 8 mm., width 3.5 mm.

Distribution.—New Brunswick.
Host plant.—*Abies balsamea.*

This subspecies is closely related to *drummondi*, as indicated by the structure of the genitalia and the costate elytra. It may be readily separated from all the members of the *fulvoguttata* group by the green color. It is a valid subspecies.

(6) *Melanophila (Phaenops) gentilis* LeConte

Melanophila gentilis LeConte, 1863, List N. Am. Coleop., p. 42.
Melanophila gentilis Horn, 1882, Trans. Am. Entom. Soc., X:105.
Melanophila gentilis Burke, 1919, Jour. Econ. Entom., XII:107.
Melanophila prasina LeConte, 1860, Trans. Am. Philos. Soc., XI:254.

Broad, robust, green above, bronze beneath. Front coarsely, closely punctate; clypeus broadly, shallowly emarginate; antennae extending to slightly beyond hind angles of prothorax, outer segments not strongly serrate, third segment almost as long as first and second together. Sides of prothorax feebly arcuate, widest in front of middle, disk somewhat rugulose; at sides closely, coarsely punctate. Elytra closely, coarsely punctate; often rugulose on disk, feebly costate near apices, which are obtuse. Body beneath sparsely punctate and clothed with short white hairs. First tarsal segment robust, slightly longer than second.

Distribution.—West coast of North America.

Host plants.—Pinus ponderosa, P. lambertiania, and *P. jeffreyi.*

This species is the most distinct of those found in our fauna. The large size, greenish color, and the broader, more robust form will serve to separate this species from any of the others.

(7) *Melanophila (Phaenops) pini-edulis* Burke

Melanophila pini-edulis Burke, 1908, Proc. Entom. Soc. Wash., IX:117–118.

Short, convex, rather densely pilose. Front moderately coarsely, closely punctate; sub-reticulate at center, distinctly pilose; not reaching hind angles of prothorax, third segment twice as long as second and only slightly longer than fourth. Prothorax one-third broader than long; disk coarsely, moderately closely punctate; basal depression distinct with a lateral depression on each side, slightly in front of base; sides feebly arcuate from base to apex, hind angles obtuse, margins obliterated in front. Elytra moderately closely, somewhat granulate-punctate, each with three large yellow spots, of which the basal one is the largest, the middle one next in size, and the apical one smallest, densely clothed with short white pile. Body beneath bronze-green, closely, coarsely punctate, and densely clothed with short while pile. First segment of hind tarsi about equal to second in length. Length 7.5 mm., width 3.5 mm.

*Distribution.—*Colorado, Arizona, Utah.

Host plants.—(Pinus edulis).

This species, as indicated by the structure of the genitalia and general facies, is closely related to *M. drummondi,* but may be readily separated from that species by the generally smaller size and the very large yellow spots of the elytra, which cover more than one-third of the total area; in *drummondi* the total area covered by the yellow spots is distinctly less than one-fifth.

(8) *Melanophila (Phaenops) fulvoguttata* (Harris)

Buprestis fulvoguttata Harris, 1829, New Eng. Farmer Ins. Inj. Veg., XLI:2.

Melanophila fulvoguttata LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:213.

Melanophila fulvoguttata Horn, 1882, Trans. Am. Entom. Soc., X:104.

Melanophila fulvoguttata Burke, 1919, Jour. Econ. Entom., XII:108.

Melanophila fulvoguttata Obenberger, 1928, Archiv Naturg., Bd. XCII, Abt. A, p. 209.

Apatura octospilota Castelnau et Gory, 1837, Monogr. Bupr., I, Apatura, p. 4.

Apatura croceosignata Castelnau et Gory, *ibid.,* p. 5.

Apatura decolorata Castelnau et Gory, *ibid.*

Melanophila guttulata Hamilton, 1889, Trans. Am. Entom. Soc., XIV:138.

Melanophila cauta Dejean, 1835, Cat. Coleop., 3d ed., p. 89.

Broad, feebly convex, black, often with small yellow elytral spots. Front closely, coarsely punctate; clypeus broadly, deeply emarginate; antennae reaching hind angles of prothorax, third segment about twice as long as second and distinctly longer than third. Pronotum broader than long, disk coarsely, feebly strigosely punctate; widest in front of middle, margins obliterated in front. Elytra not costate, closely, moderately coarsely punctate on disk; humeral region somewhat rugulose; each elytron with three small approximately equal-sized yellow spots; apices obtuse. Body beneath bronze, moderately closely, finely, punctate; sparsely clothed with short erect pile. First segment of hind tarsi distinctly, though not greatly, longer than second. Length 10 mm., width 4.5 mm.

*Distribution.—*Eastern Canada and northeastern United States.

*Host plants.—*Spruce and hemlock (*Tsuga canadensis*).

This species may be separated from *drummondi,* which it most closely resembles, by the noncostate elytra and less strigosely punctate disk of the pro-

thorax. The genitalia difference between these two species is rather distinct as shown by the plate. From *pini-edulis,* this species may be separated by the larger size and larger elytral spots. From *californica* it may be separated by the broader, flatter general shape and the rougher disk of the pronotum.

(9) *Melanophila (Phaenops) californica* Van Dyke

Melanophila californica Van Dyke, 1918, Entom. News, XXIX:54.
Melanophila californica Burke, 1919, Jour. Econ. Entom., XII:108.

Moderately convex, more elongate, bronze-black with yellow spots on the elytra. Front closely, rather finely punctate; clypeus broadly, shallowly emarginate; antennae about reaching hind angles of prothorax, third segment about twice as long as second and distinctly longer than third. Pronotum widest at base, sides very feebly arcuate, margins obliterated in front; disk smoothly, closely, coarsely punctate; hind angles obtuse. Elytra closely, coarsely punctate; somewhat granulate on disk; often each with three small equal-sized yellow spots; apices obtuse. Body beneath blue-green; closely, moderately coarsely punctate; clothed with long white hairs. First segment of hind tarsi only slightly longer than second. Length 7–.9 mm., width 3.4 mm.

Distribution.—California.
Host plants.—Many pines, especially *ponderosa* and big-cone spruce.

This species may be separated from *fulvoguttata* by the smoother disk of the pronotum, more finely punctate front, smaller size, and more linear shape. From *drummondi* it may be separated by the absence of elytral costae, smaller size, more linear shape, and the absence of rugulose punctation on the disk of the prothorax.

(10) *Melanophila (Phaenops) drummondi* Kirby

Buprestis drummondi Kirby, 1837, Richardson's Fauna Bor.-Am., IV:159.
Apatura drummondi Castelnau et Gory, 1841, Monogr. Bupr., I, Apatura, p. 3.
Melanophila drummondi LeConte, 1857, Proc. Acad. Nat. Sci. Phila., IX:7.
Melanophila drummondi LeConte, 1859, Trans. Am. Philos. Soc., XI:104.
Buprestis umbellatarrum Kirby, 1837, Richardson's Fauna Bor.-Am., IV:159.
Melanophila guttulata Mannerheim, 1853, Bull. Soc. Nat. Imp. Moscow, XXVI:221.
Melanophila drummondi ab. *tristicula* Obenberger, 1928, *ibid.,* pp. 209–210.

Robust, flattened, black or bronze. Front coarsely punctured, often with callosities; clypeus broadly emarginate; antennae blue-black, third segment elongate, almost as long as following two. Prothorax widest near apex, sides feebly arcuate, lateral margins usually almost entire, disk strigosely punctured, sides coarsely and densely punctate. Elytra densely granulate-punctate, with three fine, rather vague costae, margins near apex not serrulate; usually three yellow spots on each elytron; apices obtuse. Body beneath shining, moderately punctate, and clothed with long white pile. First segment of hind tarsae distinctly longer than second.

Distribution.—California, Oregon, Arizona.
Host plants.—Spruces, firs, and pines.

As shown by the genitalia, this species is quite distinct and may be separated by the use of this structure from *fulvoguttata* and *californica.* This species may be separated from *arcuata* Fall by the more strigosely punctured side of the pronotum. There appears to be a number of somewhat divergent forms within the realm of this species. In the series studied there is noticeable variability in the placement of the yellow spots of the elytra, and in some individuals they are entirely lacking. Two specimens from northern California

are a copper color without spots, whereas two from Utah are smaller than average and have larger spots. A study of the genitalia indicates that these are all of the same species.

Dr. Obenberger, in 1928, described a species of *Melanophila* apparently closely related to, if not synonymous with, *drummondi*. Because no specimens of this species have been available for study, the original description will be included here for the sake of completeness.

Melanophila LeConti Obenberger

"Hab.: Californien: Tahoe; Grass Valley. Long.: 10–11,2, Lat: 3,5–4,5 mm.

"Diese Art kommt in den Sammlungen zwischen den *Drummondi ab tristicula* m. vor. Sie ist von ähnlicher Form, aber robuster und brieter gebaut, viel dunkler, rein schwarz, stets einfarbig, mehr abgeglättet und stärker glänzend, oben auf den Flugeldecken mit Spuren von kurzen Härchen; die stirn ist runzeliger, in der Mitte mit drei abgeglätteten Reliefen, am Scheitel mit einem kleinen, langlichen Reliefchen, sie ist deutlich länger, der Clypeus ist tiefer ausgerandet, die Fuhler sind länger und schlanker. Der Halsschild ist viel breiter, seitlich viel stärker gerundet, die Skulptur ist ganz abweichend, sie steht etwa in der Mitte zwischen der der *Drummondi* und der *fulvoguttata* und sie bestecht in der Mitte aus einer viel weniger dichten, queren, viel stärkeren Runzelung. Vorderrand des Halsschildes, der beir *Drummondi* fast bogenförmig ausgerandet erscheint, ist hier stark doppelbuchtig, mit sehr deutlichem, breiten Mittellappen. Der Basallappen des Halsschildes, vor dem Schildchen ist breiter. Die Unterseite ist glänzender, etwas spärlicher behaart. Das Analsternit ist zur Spitze viel stärker verengt, gewölbter. Die ganze Unterseite ist glänzender und viel stärker, gröber punktiert, kupferig. Die Mitte des Basalsternites ist schmal abgeglättet und unpunktiert. Die Flügeldecken zeigen in der Hinterhälfte stets Spuren von drei Längsrippen. Der Halschild ist bei dieser Art viel breiter als bei den ähnlichen Formen, wie z. B. *fulvoguttata* und *Drummondi*. Die männlichen Kopulationsorgane von allen diesen drei ' Arten sind, was die Form der Parameren anbelangt, verschieden gebaut."

(11) *Melanophila (Phanenops) arcuata* Fall

Melanophila arcuata Fall, 1931, Pan.-Pac. Entom., VIII:83.

Because no specimens of this species have been available for study, Dr. Fall's description and comments are inserted here.

"Rather broadly oblong oval, subdepressed; black, head and body beneath with distinct aëneous luster, pronotum with faint traces of the same, elytra not visibly aeneous, upper surface with very sparse, short and inconspicuous pale hairs, integuments moderately shining.

"Head densely punctate, front with a short fine median carina between two smoother, raised callus-like spots; occiput with a fine median impressed line.

"Prothorax about three-fifths as long as wide, widest at middle, sides as seen from above nearly evenly arcuate, the base very little wider than the apex; hind angles sharply defined and slightly obtuse; surface densely punctate without any well-defined median transverse strigosity, disk with an impression each side at about the middle of the length, lateral marginal line obsolete for a short distance in front.

"Elytra oval, width five-eighths as great as the sutural length, base slightly wider than the base of the thorax, sides arcuate throughout, apices rounded and finely serrate. Punctures close moderately coarse becoming subgranulose at base and with a tendency toward an arrangement in transverse lines; each elytron with two broad ill-defined discal impressions and three obtuse subcostaform lines of which the one nearest the suture is longest but not reaching either base or apex.

"Prosternum broadly, feebly emarginate in front, the intercoxal process suddenly narrowed at tip; surface very densely punctate and with erect cinereous hairs; metasternum and abdomen more sparsely punctate.

"Length 9.6 mm., width 4.25 mm.

"Arizona: Grand Canyon of the Colorado (north rim), August 18, 1929. A single example of uncertain sex collected by Miss Edith Mank of Lawrence, Massachusetts, who kindly permits me to retain the type.

"This species is probably closest to *drummondi* but lacks the strigosity of the pronotal *surface characteristic of that species*, and the sides of the thorax are more evenly arcuate and more narrowed behind."

Subgenus XENOMELANOPHILA Sloop, n. subgen.

Broad, flattened; elytra strongly marked with yellow linear maculation. Pronotum with raised, polished, dorsal callosities. Middle coxae without sensory pits contiguous to the lateral margins. The anal veins of the wings pigmented only at base. Apices of the male genitalia not produced into a spine parallel to the margin of the aedeagus.

Genotype *Melanophila miranda* LeConte

This subgenus is immediately separated from the true *Melanophila* by the absence of the mesothoracic sensory pits though it has the general facies of that group. The genitalia and the absence of pigmentation in the anal veins of the wings separate it from the subgenus *Phaenops*. As the Mexican fauna becomes better known, sufficient evidence may be accumulated for completely separating this group from the genus *Melanophila*.

Melanophila (Xenomelanophila) miranda LeConte

Phaenops miranda LeConte, 1854, Proc. Acad. Nat. Sci. Phila., VI:83.
Melanophila miranda LeConte, 1859, Trans. Am. Philos. Soc. (2), XI:212.
Melanophila miranda Horn, 1882, Trans. Am. Entom. Soc., X:102.

Front closely, coarsely punctate; with five raised smooth callosities; clypeus broadly, moderately acutely emarginate; antennae extending to slightly behind hind angles of prothorax, third segment twice as long as second and distinctly longer than fourth. Prothorax broader than long, widest at middle, margins obliterated in front, disk closely, very coarsely punctate, with seven raised, smooth callosities. Elytra at base distinctly wider than prothorax, smooth, rather finely, somewhat sparsely punctate; margins serrate near apices, which are subacuminate; the yellow pattern covering about one-half the total surface area. Body beneath green, closely, moderately granulate-punctate; first segment of hind tarsi as long as following three. Length 14 mm., width 5 mm.

Distribution.—New Mexico.
Host plants.—Unknown.

M. miranda may be separated from all the species of our fauna by the callosities of the head and prothorax; from the subgenus *Melanophila* it may be separated by the absence of the mesothoracic pits, and from all the *Phaenops* by the more flattened general shape and stronger, more linear yellow markings of the elytra.

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A STUDY OF THE GENUS GLYPTOSCELIS LeCONTE IN AMERICA NORTH OF MEXICO

(COLEOPTERA, CHRYSOMELIDAE)

BY

N. L. H. KRAUSS

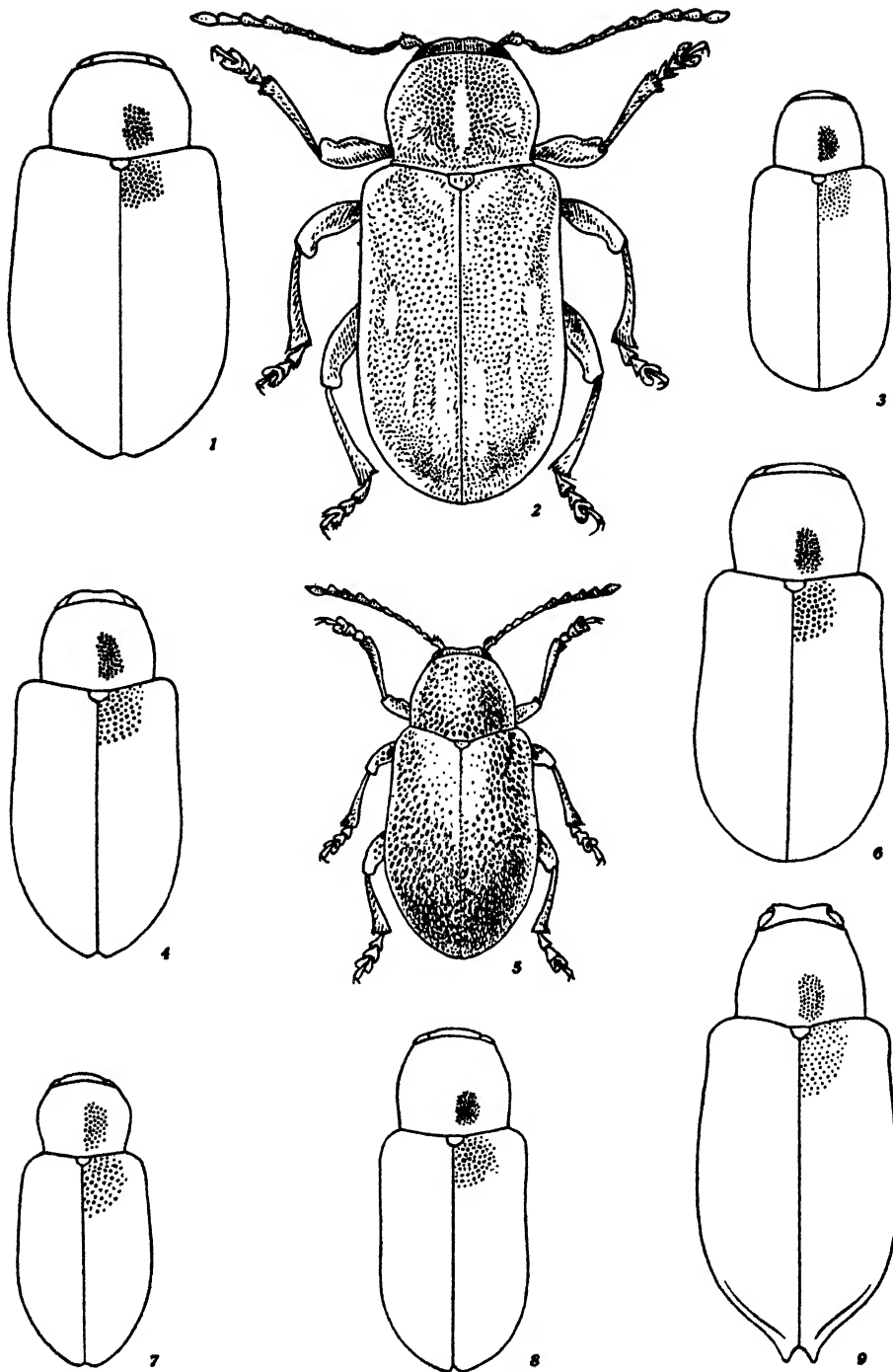# CONTENTS

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A STUDY OF THE GENUS GLYPTOSCELIS LeCONTE IN AMERICA NORTH OF MEXICO
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INTRODUCTION

THIS PAPER is planned as a revision of the species of the chrysomelid genus *Glyptoscelis* occurring in America north of the Mexican border. The last revision of the group was made by Horn in 1892. As a number of new forms have been described since the appearance of Horn's paper, and as several errors have appeared in the literature because of rather inadequate descriptions of some species, a revision of the group is surely advisable. The genus contains several species which have attained some economic importance because of their attacks on various crops. In the present paper detailed descriptions of the previously known North American species are given and several new forms are described. The writer has been fortunate in having access to the extensive series of this genus in the collection of the California Academy of Sciences in San Francisco.

It is a pleasure to express my sincere appreciation to Professors E. C. Van Dyke, S. F. Light, and S. B. Freeborn, all of the University of California, for valuable suggestions offered in the preparation of this paper and for reading the manuscript. I am also greatly indebted to Dr. R. L. Webster, Professor of Entomology at Washington State College, and to Mr. E. A. Chapin, Curator of the Division of Insects, United States National Museum, for the loan of needed specimens. The skillfully drawn illustrations have been made by Mrs. Frieda Abernathy.

Unless otherwise indicated, the distributional records are taken from specimens in the collection of the California Academy of Sciences.

DISTRIBUTION AND BIOLOGY

The genus *Glyptoscelis* is one of about a score forming the tribe Myochroini of the subfamily Eumolpinae, family Chrysomelidae. The Myochroini are widely distributed throughout the world and reach their greatest development in the Americas. Three genera, *Myochrous, Glyptoscelis,* and *Colaspidea,* are found in America north of Mexico. *Glyptoscelis* is a purely American genus, containing twenty-three species and three subspecies. Of these, twelve species and three subspecies occur in the United States, three are found in Cuba, and one each in Santo Domingo, Mexico, Nicaragua, Colombia, Venezuela and Trinidad, Brazil, Paraguay, and Chile. The genus is most highly developed in the western United States, where seven species and three subspecies are found.

Very little is known of the biology of the species of this genus. *G. squamulata* has been recorded as damaging grape and peach orchards. The adults rest in concealment during the day and at sundown come out to feed on the tender leaves of young shoots. The larvae have been taken deep underground, feeding on roots. *G. longior* apparently feeds normally on sagebrush, but since the development of agriculture in its range it has spread to such trees as apple, peach, pear, and cherry. A number of species are apparently more or less restricted to coniferous trees.

Genus GLYPTOSCELIS LeConte

Eumolpus Weber, 1801, Observ. Entom., p. 28.
Glyptoscelis LeConte, 1859, Proc. Acad. Nat. Sci. Phila., 11:81.

Oblong-oval, surface distinctly punctate, clothed with hairlike to scalelike pubescence. Head moderately convex; eyes emarginate opposite bases of antennae; antennae fairly long and slender, segments 7–11 distinctly stouter than segments 2–6. Prothorax convex, distinctly narrower than elytra. Scutellum fairly large, moderately punctate and pubescent. Elytra fairly elongate, convex, slightly flanged about outer border, humeral umbones distinct. Prosternum much longer than wide, narrowed between the coxae. Tibiae longitudinally sulcate, expanded at apices, without teeth at apices; claws more or less strongly cleft (except in *G. cryptica*).

Glyptoscelis may be distinguished from *Myochrous*, which it resembles somewhat, by the absence of dentation on the sides of the thorax, the absence of teeth near the apices of the front tibiae, and by the cleft claws (except in *G. cryptica*).

Glyptoscelis albida LeConte, the species from which LeConte drew up the generic characters, is designated as the genotype.

KEY TO THE SPECIES

1. Elytra with distinct circumscutellar depression.............................. 2
   Elytra convex at base... 5
2. Vestiture of elytra moderately sparse but evenly distributed...................... 3
   Vestiture of elytra of brownish hairs with scattered patches of longer white hairs.....
   illustris
3. Prothorax narrowing at base, thoracic punctation oval...................*pubescens*
   Prothorax not narrowing at base, thoracic punctation round...................... 4
4. Smaller, 6–7 mm. long, moderately coarsely punctate, vestiture moderately long.......
   sequoiae
   Larger, 8–9 mm. long, more coarsely punctate, vestiture longer......*sequoiae vandykei*
5. Vestiture of long, hairlike scales.. 6
   Vestiture of broad, rather short scales.......................................11
6. Thorax slightly narrowed at base.. 7
   Thorax not narrowed at base.. 8
7. Robust, vestiture ferruginous...*barbata*
   Slender, vestiture white...*parvula*
8. Elongate, clothed with long fine pubescence, thoracic punctation quite shallow.*prosopis*
   Clothed with moderately broad hairlike scales, thoracic punctation deep, distinct.... 9
9. Robust, pubescence of white moderately broad hairlike scales.................*albida*
   Less robust, pubescence of finer, slightly longer, usually intermixed brown and white
   scales...10
10. Thoracic punctation rather coarse, eyes shallowly emarginate opposite bases of antennae
    albida yosemitae
    Thoracic punctation finer, more widely spaced, eyes deeply emarginate opposite bases of
    antennae ....*albida diabola*

1. *Glyptoscelis illustris* Crotch
Figure 2

Glyptoscelis illustris Crotch, 1873, Proc. Acad. Nat. Sci. Phila., 25:35–36. Horn, 1892, Trans. Am. Entom. Soc., 19:202.

Oblong-oval, robust, broadly rounded posteriorly, burnished cupreous, sparsely clad with fine short brown hairs, slightly longer white hairs forming border around margins of prothorax and elytra and patches at outer hind angles of pronotum and on the elytra. Head moderately convex, with distinctly impressed longitudinal median line, moderately punctate, punctures well defined and the majority separated by distances about equal to their diameters, pubescence brownish with whitish patches sometimes present between the eyes; eyes distinctly emarginate opposite bases of antennae; antennae rufous to dusky, sparsely clothed with fine white hairs; palpi fulvous to dusky, darker at apices, clad with a few fine white hairs. Prothorax about three-fourths as long as broad, broadest at middle, narrowing slightly posteriorly, apex broadly arcuate, base slightly lobed at middle, disk somewhat more coarsely punctate than head, punctures separated by distances equal to their diameters. Scutellum transverse, with a few punctures and brownish hairs. Elytra more than two-thirds as broad as long, broadly rounded posteriorly, with distinct circumscutellar depression, humeral umbones prominent, punctation less closely placed than on prothorax, punctures finer posteriorly. Abdomen more closely punctate than elytra, clothed with white pubescence. Legs aeneous, clothed with whitish hairs, claws cleft to about the middle, inner division small and weak. Length 9–11 mm., breadth 4.5–5.5 mm.

This species is the largest of the genus in the United States fauna. It can be readily distinguished from the other species by the distinctive pattern formed by the white pubescence on the prothorax and elytra.

Type locality.—"California (Horn), Oregon (Walsingham)."

Distribution.—CALIFORNIA—Calaveras Co.: Mokelumne Hill; Inyo Co.: Argus Mountains (Riley, 1893); Madera Co.: Bass Lake (R. P. Allen Coll.); Placer Co.: Forest Hill; Trinity Co.: Carrville; Tuolumne Co. OREGON (Horn, 1892).

Host.—Yellow pine, *Pinus ponderosa* Dougl. (Blaisdell, 1921).

2. *Glyptoscelis pubescens* (Fabricius)

Eumolpus pubescens Fabricius, 1777, Gen. Ins. Mant., p. 220.
Eumolpus hirsutus Gmelin, 1788, Gmel. ed. Linn., 1:4:1703.
Eumolpus hirtus Olivier, 1808, Entomologie, 6:906.
Eumolpus pini Say, 1827, Jour. Acad. Nat. Sci. Phila., 5:295.
Glyptoscelis pubescens Horn, 1892, Trans. Am. Entom. Soc., 19:203.
Glyptoscelis hirtus Felt, 1902, U. S. Div. Entom. Bull. (n.s.), 31:64.

Oblong-oval, robust, broadly rounded posteriorly, fuscous with an aeneous sheen, somewhat sparsely clothed with intermixed white and brownish pubescence. Head with slightly raised or impressed longitudinal median line, punctation coarse and distinct, punctures separated by distances equal to about half their diameters, clothed with intermixed white and brown hairs; eyes moderately emarginate opposite bases of antennae; antennae dusky, darker toward apices, sparsely clothed with fine white hairs; palpi fulvous to fuscous, with a few fine white hairs. Prothorax slightly more than two-thirds as long as broad, broadest at middle, narrowing slightly to base, sides strongly arcuate, apex and base broadly arc-

uate, disk coarsely punctate, punctures oval, separated by distances about equal to half their lesser diameters. Scutellum large, slightly transverse, with a few small punctures and fine intermixed white and brownish hairs. Elytra about two-thirds as broad as long, with distinct circumscutellar depression, humeral umbones strong, punctation finer than on prothorax, punctures round, separated by distances about equal to their diameters. Abdomen moderately punctate, punctures separated by distances equal to their diameters, moderately clothed with rather fine white or brownish hairs. Legs fuscous, sparsely clothed with fine white hairs, claws moderately strongly cleft near the middle, inner division about one-third as long as outer. Length 7.5–9.5 mm., breadth 3.5–5 mm.

This species somewhat resembles *illustris* in general form. It is smaller, however, and does not have the characteristic pubescence pattern of the latter, being uniformly clothed with intermixed brown and white hairs. The thoracic punctation is oval in shape, a character which it shares with *squamulata*. Felt (1906) has illustrated this species.

Distribution.—ONTARIO to GEORGIA (Leng, 1920). CONNECTICUT (Britton, 1920). DISTRICT OF COLUMBIA (Ulke, 1902). MASSACHUSETTS—Suffolk Co.: Forest Hills. NEW JERSEY (Smith, 1910)—Gloucester Co.: Malaga; Ocean Co.: Lakehurst. NEW YORK (Leonard, 1928)—Erie Co.: Buffalo. PENNSYLVANIA—Dauphin Co. VIRGINIA—Spotsylvania Co.: Fredericksburg. Crotch (1873) has recorded *pubescens* from Oregon, but this is probably an error.

Hosts.—Pine (Ulke, 1902; Felt, 1906), hemlock (Beutenmuller, 1890), spruce (Felt, 1906).

3. *Glyptoscelis barbata* (Say)

Eumolpus barbatus Say, 1826, Jour. Acad. Nat. Sci. Phila., 5:2:296.
Glyptoscelis barbata Horn, 1892, Trans. Am. Entom. Soc., 19:203.

Oblong-oval, robust, broadly rounded posteriorly, shining fuscous, somewhat sparsely clothed with wiry ferruginous pubescence. Head with feebly impressed longitudinal median line, coarsely punctate, punctures separated by distances equal to half their diameters; eyes slightly emarginate opposite bases of antennae; antennae ferruginous, sparsely clothed with fine white hairs; palpi fulvous to fuscous, darker at apices, with a few fine white hairs. Prothorax slightly broader than long, broadest at middle, narrowing slightly posteriorly, sides moderately arcuate, disk coarsely punctate, punctures separated by distances somewhat less than half their diameters. Scutellum slightly transverse, with a few small punctures and fine ferruginous hairs. Elytra about two-thirds as broad as long, without circumscutellar depression, humeral umbones prominent, surface coarsely, not deeply punctate, punctures separated by distances equal to their diameters, pubescence coarser than on prothorax, of intermixed white and ferruginous hairs. Abdomen more distinctly punctate than elytra, punctures separated by distances equal to their diameters, pubescence much finer than on elytra, whitish. Legs sparsely clad with fine white hairs, claws deeply cleft, inner division slightly shorter than outer. Length 5.5–7.5 mm., breadth 3.5–4.5 mm.

This species may be separated from *pubescens* by its smaller size and more robust form and by the absence of a circumscutellar depression.

Distribution.—Northern Atlantic region (Horn, 1892). CONNECTICUT (Britton, 1920). DISTRICT OF COLUMBIA (Ulke, 1902). INDIANA (Blatchley, 1910). NEW JERSEY (Smith, 1910). NEW YORK (Leonard, 1928; Felt, 1906). PENNSYLVANIA—Allegheny Co.: Allegheny; Dauphin Co.: Hummelstown.

Hosts.—Pine (Ulke, 1892), hickory (Blatchley, 1910; Felt, 1906), wild grape (Blatchley, 1910).

4. *Glyptoscelis liebecki* Blatchley

Glyptoscelis liebecki Blatchley, 1910, Coleop. Indiana, p. 1137.

Oblong-oval, moderately robust, ferruginous, clothed with broad prostrate white or inter-

mixed white and fulvous scales. Head with feebly impressed longitudinal median line, some-what coarsely punctate, punctures separated by distances equal to a little less than half their diameters, densely clothed with whitish pubescence; eyes distinctly emarginate opposite bases of antennae; antennae fulvous to rufous, sparsely clothed with fine white hairs; palpi fulvous with a few fine white hairs. Prothorax slightly broader than long, not narrowed at base, sides evenly arcuate, apex and base broadly rounded, disk coarsely and deeply punctate, punctures separated by distances equal to half their diameters. Scutellum transverse, with a few punctures and fine white hairs. Elytra about two-thirds as broad as long, humeral umbones distinct, surface more finely punctate than prothorax, punctures separated by distances a little greater than their diameters, pubescence broader than that of prothorax. Abdominal punctation more closely placed than that of elytra, pubescence more hairlike. Legs ferruginous, moderately clothed with white hairs, claws strongly cleft, inner division distinctly shorter than outer. Length 7–9 mm., breadth 4–4.5 mm.

This species belongs near *barbata*, but it can be separated from that species by its larger size, ferruginous surface, and shorter, distinctly broader scale-like pubescence. Blatchley (1910) has illustrated this species.

Type locality.—Knox, Martin, and Posey counties, Indiana.
Distribution.—ILLINOIS—southern (U. S. Nat. Mus.). INDIANA—Knox, Martin, and Posey counties (Blatchley, 1910).

5. *Glyptoscelis prosopis* Schaeffer
Figure 8

Glyptoscelis prosopis Schaeffer, 1905, Brooklyn Mus. Sci. Bull., 1:7:169–170.
Elongate oblong-oval, moderately rounded posteriorly, piceous with aëneous tinge, moderately evenly clothed with fine white pubescence. Head without longitudinal median line, shallowly punctate, punctures separated by distances about equal to half their diameters, surface minutely rugose; eyes deeply emarginate opposite bases of antennae; antennae fulvous, outer segments darker, clad with very fine white hairs; palpi fulvous to fuscous, darker at apices, with a few fine white hairs. Prothorax slightly broader than long, apex broadly arcuate, sides broadly evenly arcuate, disk coarsely shallowly punctate, punctures separated by distances equal to less than half their diameters, moderately pubescent, hairs long, fine, and white. Scutellum transverse, with a few punctures and fine white hairs. Elytra about two-thirds as broad as long, without depressed circumscutellar area, humeral umbones distinct, surface coarsely punctate, punctures separated by distances equal to their diameters, pubescence coarser than on prothorax, white. Abdomen obscurely punctate, surface minutely rugose, more densely pubescent than elytra. Legs fulvous to dusky, sparsely clothed with fine white hairs, claws deeply cleft, inner division somewhat shorter than outer. Length 6–8.5 mm., breadth 3–4 mm.

This species can be readily distinguished from *albida*, which it most closely resembles, by its elongate form, coarse shallow punctation, and fine pubescence.

Type locality.—Brownsville, Texas.
Distribution.—TEXAS—Cameron Co.: Brownsville (Schaeffer, 1905).
Hosts.—Mesquite, *Prosopis juliflora* DC. (Schaeffer, 1905); *Acacia farnesiana* (E. G. Linsley, collector).

6. *Glyptoscelis albida* LeConte
Figure 1

Glyptoscelis albidus LeConte, 1859, Proc. Acad. Nat. Sci. Phila., 11:81.
Glyptoscelis albida Horn, 1892, Trans. Am. Entom. Soc., 19:203.
Oblong-oval, robust, moderately rounded posteriorly, shining piceous, rather densely clothed with white hairs. Head without impressed longitudinal median line, fairly closely

punctate, punctures irregularly placed, those between the eyes somewhat larger and more widely placed than the others; eyes deeply emarginate opposite bases of antennae; antennae ferruginous to piceous, sparsely clad with fine white hairs; palpi fuscous to piceous, darker at apices, with a few fine white hairs. Prothorax distinctly broader than long, not narrowed at base, sides evenly arcuate, apex moderately arcuate, base broadly lobed at middle, disk rather coarsely punctate, punctures generally separated by distances distinctly less than half their diameters. Scutellum transverse, with a few punctures and fine hairs. Elytra slightly more than two-thirds as broad as long, moderately rounded posteriorly, without circumscutellar depression, humeral umbones distinct. Abdomen moderately punctate, punctures more closely placed posteriorly, pubescence finer than on elytra, white. Legs fuscous to piceous, sparsely clad with rather fine white hairs, claws moderately strongly cleft at middle, inner division much shorter than outer. Length 7–9.5 mm., breadth 3–5.5 mm.

This species has contained, up to recent times, a heterogeneous and widely distributed group of distinct forms. The writer believes *longior,* which Horn placed as a synonym of *albida,* to be a distinct species. Two other forms are here described as new subspecies. *Albida* is the most robust of the species treated in this paper and has a pronouncedly transverse prothorax.

Type locality.—Tejon, California.

Distribution.—CALIFORNIA—Kern Co.: Lebec, Mount Pinos, Tejon; San Bernardino Co.: Forest Home; Tulare Co.: Visalia.

Host.—Poplar (Visalia, California).

6a. *Glyptoscelis albida yosemitae,* n. subsp.

Somewhat similar in size and general appearance to the typical form, but differing in being distinctly less robust and in that the somewhat less dense pubescence is of slightly shorter and finer intermixed brown and white hairs. The eyes are more shallowly emarginate opposite the bases of the antennae than in typical *albida.* Length 8–9.5 mm., breadth 4–5 mm.

Type and paratypes (Yosemite Valley, California) in the collection of the California Academy of Sciences, San Francisco.

Distribution.—CALIFORNIA—Fresno Co.: Stevenson Creek; Tulare Co.: Atwoods Mill; Yosemite Valley.

Hosts.—Yellow pine, *Pinus ponderosa* Dougl. (Yosemite Valley, California); incense cedar, *Libocedrus decurrens* Torr. (Stevenson Creek, California).

6b. *Glyptoscelis albida diabola* Krauss, n. subsp.
Figure 4

Much less robust than the typical form, less broadly rounded posteriorly, color more aëneous, thoracic punctation finer and more widely placed, pubescence of finer usually intermixed brown and white hairs. Length 6.5–9.5 mm., breadth 3.5–4.5 mm.

Type and paratypes.—Mount Diablo, California; in the collection of the California Academy of Sciences, San Francisco.

Distribution.—CALIFORNIA—Alameda Co.: hills behind Oakland, Niles Canyon; Contra Costa Co.: Mount Diablo; Monterey Co.: Paraiso Springs.

7. *Glyptoscelis longior* LeConte
Figure 3

Glyptoscelis longior LeConte, 1878, U. S. Geol. Surv. Bull., 4:3:462.
Glyptoscelis albida Horn, 1892, Trans. Am. Entom. Soc., 19:203.

Oblong-oval, not robust, broadly rounded posteriorly, piceous with an aëneous sheen, clothed with whitish to fulvous hair, vittate on elytra. Head with slightly impressed longi-

tudinal median line, punctures distinct, separated by distances about equal to their diameters, more closely placed between the eyes; eyes broadly emarginate opposite bases of antennae; antennae long, gradually enlarging to apex, fulvous to fuscous, darker towards apices, sparsely clad with fine white hairs; palpi fulvous to fuscous, with a few fine white hairs. Prothorax slightly broader than long, slightly narrowed anteriorly, apex moderately arcuate, base slightly, evenly arcuate, disk moderately finely punctate, punctures separated by distances somewhat less than their diameters. Scutellum slightly transverse, with a few small punctures and fine white hairs. Elytra somewhat less than two-thirds as broad as long, without circumscutellar depression, humeral umbones distinct, punctation somewhat finer than on prothorax, finer and more widely spaced posteriorly, pubescence of white and fulvous hairs, usually arranged so as to give a faint striped appearance. Punctures on abdomen separated by distances about equal to their diameters, pubescence slightly finer than on elytra, white. Femora aëneopiceous, tibiae and tarsi dusky, sparsely clothed with white hairs, claws cleft to about middle, inner division about two-thirds length of outer. Length 5.5–7 mm., breadth 3–3.5 mm.

Horn (1892) has declared this species to be a synonym of *albida*, but the writer cannot agree with this interpretation. *Longior* is easily distinguished from *albida* by its smaller size, distinctly less robust form, much less transverse prothorax, finer pubescence, and faintly vittate-elytra. This species has been referred to as *alternata* by some of the workers in the Northwest.

Type locality.—Atlanta, Idaho.

Distribution.—BRITISH COLUMBIA—Summerland (State College of Washington Collection), Vernon. COLORADO—Delta Co.: Paonia. IDAHO—Elmore Co.: Atlanta (LeConte, 1878). NEVADA—Washoe Co.: Steamboat Springs. OREGON—Baker Co.: Sparta; Harney Co.: Steen Mountains; Mountains west of La Grange (La Grande ?). WASHINGTON—Chelan Co.: Wenatchee (State College of Washington Collection); Yakima Co.: Prosser; Whitman Co.: Almota and Pullman (State College of Washington Collection), Wawawai. WYOMING—Teton Co.: Grand Teton National Park.

Hosts.—Sage, apple, peach, pear, sunflower (Yothers, 1916), cherry. Yothers has published a few notes on this species and illustrated the eggs under the name *alternata*.

8. *Glyptoscelis sequoiae* Blaisdell

Glyptoscelis sequoiae Blaisdell, 1921, Stanford Univ. Publ. Biol. Sci., 1:3:195–196.

Oblong-oval, broadly rounded posteriorly, cupreous, sparsely and evenly clothed with recumbent fulvous pubescence. Head with impressed longitudinal median line, somewhat coarsely punctate, more so between bases of antennae, majority of punctures separated by distances equal to half their diameters; eyes deeply emarginate opposite bases of antennae; antennae ferruginous, darker at apices, sparsely clad with fine pubescence; palpi ferruginous to dusky, with a few fine hairs. Prothorax slightly broader than long, sides rather evenly arcuate, moderately convergent anteriorly, apex broadly arcuate, base slightly lobed at middle, disk somewhat coarsely punctate, punctures separated by distances equal to half their diameters, clothed with fulvous hairs, denser and coarser laterally. Scutellum slightly transverse, surface with a few small punctures and fine hairs. Elytra less than two-thirds as broad as long, broadly rounded posteriorly, with distinct depression about scutellum, humeral umbones distinct, surface less closely and coarsely punctate than prothorax, punctures somewhat finer posteriorly, evenly clothed with fulvous pubescence. Abdomen distinctly punctate, punctures separated by distances equal to their diameters, pubescence finer and slightly longer than on elytra. Legs rufous, clothed with fine hairs, claws moderately cleft, inner division much shorter and smaller than outer. Length 6–8 mm., breadth 3–4 mm.

This species may be distinguished from *longior*, which it most closely resem-

bles, by the presence of a distinct circumscutellar depression, by the stouter antennae, and by the finer pubescence, which is not vittate on the elytra.

Type locality.—Cazadero, California.

Distribution.—CALIFORNIA—Calaveras Co.; Eldorado Co.: Bijou, Fallen Leaf Lake, Glen Alpine; Fresno Co.: Huntington Lake; Humboldt Co.; Inyo Co.: Bishop; Lassen Co.: Facht, Martius Springs, Norval Flats; Mariposa Co.; Nevada Co.: Graniteville, Truckee; Placer Co.: Cisco, Dutch Flat, Forest Hill; Plumas Co.: Meadow Valley; Sierra Co.: Gold Lake; Siskiyou Co.: McCloud, Shasta Springs; Sonoma Co.: Cazadero, Guerneville; Trinity Co.: Carrville, Nash Mine; Tulare Co.: Atwoods Mill, Visalia; Yosemite Valley. IDAHO—Latah Co.: Moscow Mountains (State College of Washington Collection). NEVADA—Ormsby Co.: Carson City. OREGON—Klamath Co.: Crater Lake. WASHINGTON—Bird Creek, Mount Adams (State College of Washington Coll.).

Hosts.—Foliage of redwood, *Sequoia sempervirens* (Lamb.) Endl. (Blaisdell, 1921); cedar (Placer and Tulare Cos., California); mountain juniper (E. C. Van Dyke); pear (Nevada Co., California).

8a. *Glyptoscelis sequoiae vandykei* Krauss, n. subsp.
Figure 6

Differing from typical *sequoiae* by being larger, more coarsely punctate on the prothorax, and clothed with distinctly longer pubescence. The color is aëneopiceous and the vestiture is of long, fine intermixed white and fulvous hairs. Length 8–9 mm., breadth 4–4.5 mm.

Type and paratypes (Klamath Falls, Oregon) in the collection of the California Academy of Sciences, San Francisco. I take great pleasure in naming this subspecies after Dr. E. C. Van Dyke, who has done so much in making known the coleopterous fauna of the West.

Distribution.—OREGON—Klamath Co.: Crater Lake, Klamath Falls.

9. *Glyptoscelis parvula* Blaisdell
Figure 7

Glyptoscelis parvulus Blaisdell, 1921, Stanford Univ. Publ. Biol. Sci., 1:3:196–197.

Short oblong-oval, moderately rounded posteriorly, piceous with aëneous sheen, rather sparsely and evenly clothed with moderately long whitish hairs. Head with more or less evident longitudinal median line, punctation rather coarse and irregularly placed, majority of the punctures separated by distances equal to their diameters; eyes deeply emarginate opposite bases of antennae; antennae fairly long, apical five segments rather short and broad, ferruginous to piceous, sparsely clothed with fine whitish hairs; palpi fulvous to fuscous, darker at apices, with a few fine hairs. Prothorax distinctly broader than long, broadest at middle, strongly declivious at the sides in the region of the apical angles, apex moderately arcuate, base feebly arcuate, disk distinctly and moderately coarsely punctate, punctures separated by distances about equal to their diameters. Scutellum distinctly transverse, broadly rounded posteriorly, surface with a few small punctures and fine hairs. Elytra about two-thirds as broad as long, without circumscutellar depression, humeral umbones distinct, punctation somewhat finer than on thorax, less distinct, still finer on apical declivity, punctures separated by distances equal to about twice their diameters. Abdomen somewhat more closely punctate than elytra, pubescence finer than on elytra. Legs rather short, middle and posterior tibiae slightly curved outwards at apex, rufopiceous, sparsely clothed with fine hairs, claws strongly cleft. Length 5–7.5 mm., breadth 2.5–3.5 mm.

This species most nearly resembles *sequoiae,* but is very easily distinguished from that species by the shorter elytra with less broadly rounded apex, by the

stouter antennae, and by the absence of a circumscutellar depression. It is the smallest species of *Glyptoscelis* in the United States.

Type locality.—Sacramento, California.

Distribution.—CALIFORNIA—Butte Co.: near Chico; Sacramento Co.: Courtland, Michigan Bar, Sacramento; Solano Co.: Rio Vista; Tehama Co.: Los Molinos.

Hosts.—Wild rose (Blaisdell, 1921); *Salix* sp. (Los Molinos, California).

10. *Glyptoscelis squamulata* Crotch
Figure 5

Glyptoscelis squamulatus Crotch, 1873, Proc. Acad. Nat. Sci. Phila., 25:36.

Glyptoscelis squamulata Horn, 1892, Trans. Am. Entom. Soc., 19:204.

Oblong-oval, broadly rounded posteriorly, piceous with an aëneous tinge, clothed with short, very broad white or brownish scales. Head without impressed longitudinal median line, punctation distinct, irregularly placed; eyes distinctly emarginate opposite bases of antennae; antennae fulvous to fuscous, outer segments the darkest, sparsely clad with fine white hairs; palpi fulvous to fuscous, with a few fine white hairs. Prothorax distinctly broader than long, narrowing arcuately from base to apex, apex strongly arcuate, base moderately arcuate, disk moderately coarsely punctate, punctures oval, separated by distances somewhat smaller than their lesser diameters, pubescence of broad white or brownish scales, coarser than on head. Scutellum transverse, with a few punctures and small scales. Elytra about two-thirds as broad as long, without circumscutellar depression, humeral umbones distinct, punctation less distinct and shallower than on prothorax, pubescence of broad white or brownish scales, sometimes arranged in vittae. Punctures on abdomen separated by distances equal to their diameters, pubescence somewhat finer than on elytra, white. Legs ferruginous, clothed with white pubescence, claws cleft a little in front of the middle, inner division much smaller than outer. Length 6.5–7.5 mm., breadth 3–4 mm.

A somewhat variable species characterized by the very broad, closely appressed pubescence. The thoracic punctation is oval in shape. Specimens from San Diego County and elsewhere in California show a faintly vittate arrangement of the pubescence on the elytra.

Type locality.—"California (LeConte); Oregon (Walsingham)."

Distribution.—ARIZONA—central and southern part (Brisley, 1925). CALIFORNIA—Butte Co.: Oroville; Kern Co.: Bakersfield, Cuyama Valley, Poso Creek, Tapman; Kings Co.: Hanford; Los Angeles Co.: Palmdale, Rivera, Santa Monica; Monterey Co.: Bradley, Bryson; Riverside Co.: Coachella, Indio, Palm Springs; Sacramento Co.: Sacramento; San Bernardino Co.: Colton, Lytle Creek; San Diego Co.: Descanso, Mission Valley; Tulare Co.: Woodlake; Yolo Co.: Davis. OREGON (Crotch, 1873). UTAH—Beaver Co.: Milford; Washington Co.: St. George.

Hosts.—*Artemisia heterophylla* (Oroville, California); barley, roses, wild grapes, native weeds (Brisley, 1925); grape (Nougaret, 1926); willow (Bradley, California); peach (Jacobsen, 1927).

This species in recent times has caused appreciable loss to grape growers in the Coachella Valley and peach growers in the Sacramento Valley, California, by feeding on the tender young leaves of the plants.

11. *Glyptoscelis alternata* Crotch

Glyptoscelis alternatus Crotch, 1873, Proc. Acad. Nat. Sci. Phila., 25:36.

Glyptoscelis alternata Horn, 1892, Trans. Am. Entom. Soc., 19:203.

Oblong-oval, moderately rounded posteriorly, piceous, pubescence of broad white and brownish scales arranged so as to give a rather distinct striped appearance. Head without impressed longitudinal median line, coarsely punctate, punctures irregularly spaced, ma-

jority separated by distances equal to about half their diameters, pubescence white; eyes deeply emarginate opposite bases of antennae; antennae fuscous, sparsely clothed with fine white hairs; palpi dusky to piceous, with a few fine white hairs. Prothorax slightly broader than long, slightly broader at base than at middle, sides rather evenly arcuate, disk moderately coarsely punctate, punctures separated by distances equal to half their diameters, pubescence coarser than on head, white. Scutellum transverse, moderately punctate and pubescent. Elytra two-thirds as broad as long, without circumscutellar depression, humeral umbones distinct, punctation less well defined than on prothorax, punctures irregular in size, pubescence of broad white and brownish scales in alternating vittae giving a faint striped appearance. Abdomen moderately closely punctate, clothed with white pubescence somewhat more hairlike than on elytra. Legs fuscous to piceous, moderately clothed with white pubescence, claws slightly cleft at middle, inner division much shorter than outer. Length 6–9.5 mm., breadth 3.5–4 mm.

This species is rather close to *squamulata*, but can be separated from that species by the round, instead of oval, thoracic punctation and the longer, narrower pubescence which is arranged in vittae. *Longior* has occasionally been mistaken for this species in the Northwest, but *alternata* apparently does not occur outside of southern California.

Type locality.—California.

Distribution.—CALIFORNIA—Inyo Co.: Owens Valley (Horn, 1892), Big Pine, Lone Pine; Kern Co.: Isabella (R. P. Allen Coll.). Horn (1892) has recorded this species from Wyoming, but his specimens were undoubtedly *longior*.

12. *Glyptoscelis cryptica* (Say)

Figure 9

Eumolpus crypticus Say, 1823, Jour. Acad. Nat. Sci. Phila., 3:2:449.
Glyptoscelis albicans Baly, 1865, Trans. Entom. Soc. Lond. (3d ser.), 2:334–335.
Glyptoscelis cryptica Horn, 1892, Trans. Am. Entom. Soc., 19:204.

Oblong-oval, narrowing posteriorly to an attenuated tip, ferruginous, moderately clothed with broad, short, closely appressed white hairs. Head with faintly impressed longitudinal median line, moderately punctate, punctures irregularly placed; eyes broadly emarginate opposite bases of antennae; antennae ferruginous, sparsely clothed with fine white hairs; palpi fulvous, with a few fine white hairs. Prothorax distinctly broader than long, broadest at base, sides feebly arcuate and gradually narrowed to apex, moderately finely punctate, punctures separated by distances about equal to their diameters. Scutellum transverse, with a few small punctures and fine white hairs. Elytra slightly less than two-thirds as broad as long, tip acute and slightly prolonged, the apices slightly divergent, without circumscutellar depression, humeral umbones distinct, surface not deeply punctate, the punctures separated by distances somewhat greater than their diameters. Abdomen more closely punctate than elytra, pubescence distinctly longer and finer. Legs ferruginous, clothed with white hairs, claws widely separated, absolutely simple. Length 7.5–9 mm., breadth 4.5–5 mm.

This species may easily be distinguished from the others by the acutely prolonged tip of the elytra and the absolutely simple claws. Jacoby (1882) has illustrated it.

Type locality.—"Missouri."

Distribution.—DAKOTA (Horn, 1892). KANSAS—Shawnee Co.: Topeka (U. S. Nat. Mus.). MISSOURI (Horn, 1892). Jacoby (1882) has recorded a specimen from Mexico, but this is probably an error.

Hosts.—Apple and oak (Saunders, 1883).

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DESCRIPTIONS OF NEW TRIATOMINAE
WITH A KEY TO GENERA
(HEMIPTERA, REDUVIIDAE)

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INTRODUCTION

THE BLOOD-SUCKING BUGS of the subfamily Triatominae have attracted a great deal of attention in recent years in connection with studies on the transmission of Trypanosomes. Many papers have appeared on the systematics of the group, based mainly upon the rich fauna of South America. These papers, written for the most part in the Spanish or Portuguese languages by Drs. Neiva, Pinto, Del Ponte, and Lent, give a very complex picture of the South American Triatomas, which, however, remains largely inaccessible to North American workers because the systematic papers have been published either privately or in South American medical journals that are received in only a few of the largest libraries in this country. A few references have proved of particular value during the course of the present work. These are Hussey's "Bibliographical Notice" (1922), Del Ponte's well illustrated "Catálogo descriptivo" (1930), Pinto's generic review (1931), and the recent synonymical list of Neiva and Lent (1936). Dr. Lent writes that he and Dr. Neiva are at present engaged in the preparation of a general paper in which the species are to be figured and a key given.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the generous assistance of Mr. H. G. Barber, who has long been interested in these bugs and has contributed so much to our knowledge of the group. Dr. Bruce Whitaker and Drs. Fae D. Wood and S. F. Wood have coöperated in every way, where their life-history and disease-transmission studies have been concerned. Dr. Emmanuel Dias, of the Instituto Oswaldo Cruz, was most helpful in supplying South American material at the time of his recent visit to this country. Dr. W. B. Herms and Mr. E. P. Van Duzee have very kindly offered material and suggestions which have added greatly to the scope of the work. Others who have supplied material are S. C. Bruner, C. B. Philip, Nathan Banks, C. J. Drake, F. E. Lutz, and E. T. Cresson, Jr. Types and other material have been returned to the collections from which they were borrowed and will be mentioned in the course of the paper. The illustrations were meticulously prepared by Mr. Peter Artemieff.

GENERIC RELATIONSHIPS

The higher classification of the Triatominae has become a very controversial subject since the discovery, in recent times, of a great number of new species in various parts of the world. Del Ponte's conservative lumping of a great

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variety of forms under *Triatoma* and Pinto's very artificial splitting up of the group indicate the two extremes in generic concepts which prevail at the present time. Actually these bugs exhibit a wealth of structural characters upon which a sound classification will eventually be based. Unfortunately most of these characters have been completely ignored in many of the original descriptions during the past twenty-five years. As no serious attempt at a complete classification will be possible without the very rich and diverse South American forms, it is to be hoped that in the near future a thorough re-study of these bugs will be undertaken, having as its objective a phylogenetic classification brought into accord with that of the other groups of the family Reduviidae. Such a work could not be accomplished without reference to the very large collection at the Instituto de Oswaldo Cruz in Rio de Janeiro.

Stål's admirable key to genera (1859) is still the best arrangement of triatomine groups. This master of Hemipterology seemed instinctively to place species in natural groups. One of his names, *Meccus*, has fallen, but is nevertheless a perfectly distinctive and geographically delimited group, which may yet be revived when a really satisfactory classification is proposed. Stål's genus *Lamus* (1859) was unfortunately preoccupied (Stål, 1854) and later renamed *Mestor* by Kirkaldy (1904a). This genus appears to be quite distinct from *Panstrongylus,* as pointed out by Berg (1879), and was proposed for an Argentine species with the antennae inserted near the eyes, numerous spines on the undersides of the femora, a cylindrical posterior prolongation of the scutellum, and other specified characters. Several species would appear to belong here, including *seai* and *geniculatus,* while *rufotuberculatus* and *lignarius* most certainly belong with *megistus* in the genus *Mestor.* Hence, in spite of certain alleged intermediates which more probably should be placed elsewhere, I believe *Mestor* and *Panstrongylus* are really natural groups. Pinto's *Neotriatoma* (1931) was erected for the species *circummaculata,* which Stål ran out first in his specific key (1859). The species is easily distinguished by its long third rostral segment; and a second species, *limai* Del Ponte, has since turned up; but, unless other characters are found, generic status seems scarcely warranted.

The genus *Eutriatoma* Pinto (1926) has been ignored for the present because I have not seen the genotype, *tibiamaculata* Pinto, and no characters of generic value are given in the original description or in the subsequent publications in which Pinto expresses his views and refers additional species to his "genus." That the short basal segment of the rostrum is not a good character is obvious, I believe, from the very diverse forms which Pinto was led to include within the confines of this single genus. *Arthuri* Pinto, for example, was later (1935) shown by Pinto and Lent to belong to the very distinct genus *Psammolestes* and does not even remotely resemble other members included in *Eutriatoma. Uhleri* Neiva (but not *rubida* Uhler, of which it is no more than a subspecies) was included although it approaches the type *rubrofasciata* of the genus *Triatoma* more closely than *Eutriatoma. Flavida* Neiva was likewise placed here, but it differs so strikingly from allied forms

that it might better be made the type of a new genus. Still another so-called *Eutriatoma* is separated generically in the present paper. The name *Eutriatoma* may eventually be usable because the typical South American Triatomas seem to differ in general facies and in minor characters from the Old World type of the genus *Triatoma*. However, at present, the entire genus *Eutriatoma*, unless its type proves to be distinct on other characters, should be synonymized with *Triatoma* as suggested by Del Ponte in 1930.

The distressingly large proportion of monotypic genera added since 1859 leaves us with a very anomalous disparity in the relative size of groups. This, however, is not unparalleled in other families of insects. The genus *Triatoma*, as herein understood, contains more species than all the other genera combined ; *Mestor, Panstrongylus,* and *Rhodnius* each contain about a half-dozen species; *Eratyrus, Neotriatoma,* and *Psammolestes,* two or three ; and the remaining seven genera each contain but a single species. Such a situation may be fully justified, however, as discontinuity is the essence of the generic concept regardless of relative size of groups. If, as is evidently the case here, certain species have strikingly diverged either biologically, e.g. *Psammolestes* Bergroth and *Cavernicola* Barber, geographically, e.g. *Callotriatoma* n. gen. and *Adricomius* Distant, or only structurally, e.g. *Dipetalogaster* n. gen., they must be separated systematically from the main stock if we are to have a classification at all.

<div align="center">KEY TO THE GENERA OF TRIATOMINAE</div>

1. Rostrum not surpassing level of eyes....................*Linshcosteus* Distant, 1904
   <div align="right">type *carnifex* Distant, India •</div>
   Rostrum distinctly surpassing level of eyes................................... 2
2. First rostral segment longer than second.................................... 3
   First rostral segment shorter than second................................... 4
3. First antennal segment short, not reaching apex of head. Scutellum with a subbasal, obliquely divergent tubercle on either side.....................*Belminus* Stål, 1859
   <div align="right">type *rugulosus* Stål, Colombia</div>
   First antennal segment long, surpassing apex of head. Scutellum not as above.........
   <div align="right">*Adricomius* Distant, 1903</div>
   <div align="right">type *annulatus* Distant, Samoa</div>
4. Head but little longer than broad, eyes included; with a distinct granular callosity situated behind each eye and below the ocelli. Rostrum greatly flattened............
   <div align="right">*Psammolestes* Bergroth, 1911</div>
   <div align="right">type *coreodes* Bergroth, Argentina</div>
   Head distinctly longer than broad. Rostrum subcylindrical..................... 5
5. Corium without conspicuous veins. Head strongly, almost roundly elevated dorsally at middle; ocelli situated in the suture separating off the narrowed posterior lobe of the head, which tapers to the neck........................*Cavernicola* Barber, 1937*a*
   <div align="right">type *pilosa* Barber, Panama</div>
   Corial veins distinct.. 6
6. Head very long and slender, with the antennae inserted near apex; with a more or less distinct longitudinal carina dorsally..........................*Rhodnius* Stål, 1859
   <div align="right">type *prolixus* Stål, Brazil</div>
   Head variously formed but with the antennae inserted near or behind the middle of the anteocular region or, if inserted near the apex, without a pale longitudinal carina dorsally 7

7. Posterolateral angles of pronotum distinctly produced as sharp, upturned spines, which may be rather short or very long. Posterior prolongation of scutellum sharply produced, acute, and turned upward..........................*Eratyrus* Stål, 1859

type *mucronatus* Stål, Brazil

Posterolateral angles of pronotum rounded or angular but not produced as acute spines. Scutellum not as above.. 8

8. Lateral margins of ventral plates reaching abdominal margins, the connexivum thus appearing doubly lamellately expanded......................*Dipetalogaster* n. gen.

type *maximus* Uhler, Lower Calif.

Lateral margins of ventral plates not reaching connexival margins, the connexivum thus appearing singly lamellately expanded or single plated........................ 9

9. Antennae inserted behind the middle of the anteocular region and very near the eyes; the antenniferous tubercles actually arising at anterior margins of eyes; head rather short and broad..10

Antennae inserted near, or in front of, the middle of the anteocular region. Head longer 12

10. Body densely clothed with moderately long, fine, curved, black hairs. Small species, less than 14 mm.......................................*Paratriatoma* Barber, 1938

type *hirsuta* Barber, Arizona and California

Body naked except for short, obscure hairs, especially on the venter and appendages, or, rarely, with long, curved, rather coarse hairs. Larger species, more than 20 mm.....11

11. Anterior disk of pronotum with obscure, rounded tubercles rather than spines. Scutellum prolonged posteriorly into a long, cylindrical spine. Antenniferous tubercles each with a subapical lateral spine. Front and middle femora usually with two rows of conspicuous, short, stout spines beneath. Eyes small or of moderate size...*Panstrongylus* Berg, 1879

type *guntheri* Berg, Argentina

Anterior disk of pronotum with prominent tubercles or spines. Scutellar prolongation blunt, turned up at apex. Antenniferous tubercles without conspicuous spines antero-laterally. Front and middle femora with only a single pair of subapical spines. Eyes very large, two-thirds or more the width of interocular space....*Mestor* Kirkaldy, 1904

type *megistus* Burm., Brazil

12. Head subflattened, abruptly broadened behind the eyes. Ocelli situated on posterior disk, not elevated. Femora with five or six short, stout spines along undersurface. Very small species, less than 10 mm. General coloration black with sharply contrasting red on portions of the thorax, coria, and abdomen....................*Callotriatoma* n. gen.

type *cubana* n. sp., Cuba

Head subcylindrical. Ocelli situated posterolaterally on oblique, rounded elevations. Femora with fewer short spines and these situated subapically. Size and coloration variable but always larger than above and differently colored........................13

13. Second and third segments of rostrum almost equal in length..*Neotriatoma* Pinto, 1931

type *circummaculata* Stål, Argentina

Second rostral segment always distinctly longer than third....*Triatoma* Laporte, 1832

type *rubrofasciata* Degeer, Tropicopolitan

Genus **Callotriatoma** Usinger, n. gen.

Description.—Small, elongate species with body surface granular-rugose, naked except for short hairs on the appendages. Head twice as long as broad, eyes included; subflattened; broadest behind the eyes; juga acutely produced well beyond apex of tylus; anteocular region a little more than one and one-half times as long as distance from posterior margins of eyes to posterior constriction. Eyes small. Ocelli inconspicuous, situated on disk of head among coarse granules midway between eyes and posterior constriction and directly behind two oblique, sinuate impressions. Antennae inserted a little in front of middle of anteocular region; one-eighth longer than the head; first segment not reaching apex of head; first segment less than half the length of second and a little shorter than either third or fourth,

which are subequal. Rostrum very long and slender, reaching the prosternum; second segment about as wide as diameter of front tibia; first segment less than half the length of the second and twice as long as the third.

Pronotum a little broader than long, greatly narrowed anteriorly and strongly constricted at middle; anterolateral angles distinctly produced, prominent; lateral margins each with a small tooth just before median emargination and another at humeral angles; disk anteriorly with two slightly elevated tubercles.

Scutellum a little longer than broad; posterior prolongation subcylindrical, more than half the total length of scutellum.

Connexivum moderately strongly, evenly arcuate and distinctly reflexed. Venter abruptly, sharply flattened.

Femora with four or five short, stout spines arranged singly or in pairs along undersurface.

Coloration, sharply contrasting red and black.

Genotype.—*Callotriatoma cubana* Usinger, n. sp.

Remarks.—Suggestive of the genus *Belminus* Stål in size, position of ocelli, and granulation of body surface. However, in that genus the head is longer and cylindrical; the eyes are larger; the first rostral segment is longer than the second; the pronotal disk and margins are unarmed, and the anterolateral angles are scarcely produced; the scutellum has a subbasal, obliquely divergent tubercle on either side; the connexivum above is submarginally sharply depressed; the femora possess stout spines only subapically beneath; and the coloration is dark brown to black, with connexivum alternated with ochraceous on the posterior fourth of each segment. In *Triatoma* the ocelli are situated posterolaterally on obliquely directed elevations, the head is less flattened, and there are no granular callosities behind the eyes.

Callotriatoma cubana Usinger, n. sp.

(Pl. 1)

Description.—Head with sides straight and feebly divergent anteriorly before the eyes to the short, acute, antenniferous tubercles; constricted just behind the eyes and then abruptly widened by more than one-half the width of an eye, thence roundly converging posteriorly to the smooth, strongly constricted neck; sides in front of insertion of antennae parallel, the head narrowest at this level; undersurface between the eyes smooth. Eyes small, about one-half the width of the interocular space. Ocelli smooth and polished, situated just behind two subtransverse, posteriorly convergent, narrow impressions which arise at posterior margins of eyes. Proportion of antennal segments one to four as 6:19:10:11. Proportional length of rostral segments one to three as 9:22:5. Pronotum one-fourth shorter than broad behind; less than half as broad anteriorly as posteriorly; anterior angles rather strongly produced into stout, subacute, anteriorly divergent but slightly inwardly bent spines; disk strongly, transversely impressed at middle, with two elevated but scarcely produced tubercles before middle of anterior lobe and the usual posteriorly divergent carinae connecting anterior and posterior lobes; lateral margins feebly, lamellately expanded on posterior lobe, with a small blunt tooth on either side just before the abrupt, deep emargination at middle and another on humeral angles; posterior margin a little rounded. Hemelytra almost attaining the roundly truncate tip of the abdomen; coria rather granular on outer halves, smooth near inner angles.

Color in great part black on the head, thorax, hemelytra, appendages, and abdomen both dorsally and ventrally on fifth and sixth visible segments, genital capsule, and narrow anterolateral angles of third and fourth segments. Red on rest of abdomen, on the pronotum and propleura, and on posterior two-thirds of coria. Pale testaceous along margin between

corium and membrane where the red and black are adjacent. Apical two antennal segments and tarsi brown.

Size.—Length 8.83 mm.; width (pronotum) 2.3 mm., (connexivum) 3.39 mm.

Holotype, male, collected at Loma del Gato, Cobre Range, Oriente, Cuba, at about 3000 feet elevation, July 3–7, 1936, by P. J. Darlington, Jr., and now in the Museum of Comparative Zoölogy at Harvard University.

Remarks.—This is the smallest species of Triatominae as yet described and cannot be confused with any other known insect of this group.

It is interesting that several predaceous Hemiptera from Cuba are strikingly marked with the same brilliant red and sharply contrasting black colors as are seen in *Callotriatoma*. Thus, *Apiomerus burmeisterii* Guerin and *Enicocephalus cubanus* Bruner are the only representatives of their respective genera (excepting other closely allied Antillean species) with such coloration. Too much of the literature on mimicry and warning coloration is made up of idle speculation based upon museum specimens, but suggestions from this source may be of value if they point out where field work may best be concentrated. If the species just named occur in the same area, it would appear that they would be mutually benefited by combining their efforts along a single line of sematic coloration.

Mestor humeralis Usinger, n. sp.

Description.—A moderate-sized, yellow and black species with scattered, inconspicuous, depressed hairs, which become more prominent on venter and appendages; with short, broad head; short, rounded tubercles on anterior lobe of pronotum; strongly, almost lamellately produced humeral angles; a short, humped, transversely wrinkled posterior prolongation of the scutellum; and a single pair of subapically situated, obsolescent tubercles on the femora.

Male: Head sparsely beset with very short, depressed, pale hairs; one-third longer than broad, eyes included; anteocular region almost three times as long as postocular region to posterior constriction; tylus scarcely enlarged basally; juga comparatively long, prominent and subacute, extending almost half the distance from transverse impression at level of antenniferous tubercles to apex of tylus. Eyes broad, as seen from above; a little less than half as wide as interocular space. Ocelli very prominent, situated posterolaterally on obliquely directed, smooth elevations, very close to inner posterior margins of eyes. Antennae inserted one-fourth the distance from eyes to apex of head; antenniferous tubercles actually arising from anterior margins of eyes, their outer apical angles rounded; first antennal segment not quite reaching apex of head, somewhat narrowed on posterior third; second segment almost cylindrical, beset with short, slightly curved, stiff bristles; third and fourth segments broken off. Rostrum attaining prosternum; fairly robust, about as wide at middle as thickness of front tibia; proportion of segments one to three as 37:43:15. Pronotum a little longer than head on median line, 97::85; almost one-third broader than long, 140::97; and two-thirds as broad behind as at narrow pronotal collar; anterolateral angles strongly, anteriorly produced, rounded at apices; lateral margins rounded on anterior lobe, then abruptly, deeply concave before strongly dilated humeral angles; posterior margin moderately convexly rounded, a little sinuate on either side near bases of clavi; disk moderately convex near middle, with a median impressed line longitudinally which deepens to a pit posteriorly on anterior lobe; transverse impression only feebly indicated; anterior lobe with a pair of prominent, rounded tubercles before the middle, and another, feebly elevated pair behind the middle, as well as a prominent marginal pair; posterior lobe coarsely, transversely rugose, laterally depressed with short, sublateral, longitudinal elevations and with the humeral angles strongly expanded and marginally a little reflexed. Scutellum about as broad as long; strongly elevated and anteriorly slightly produced just behind depressed base; disk smooth and polished except for an anteriorly divergent, transversely rugose longitudinal

fossa at middle; posterior prolongation short, transversely wrinkled and apically rounded or almost cordiform, strongly elevated or "humped" at base, then abruptly depressed and again turned up at apex. Hemelytra reaching almost to apex of abdomen, the costal margins subparallel, being a little convexly rounded basally, then gradually narrowed at middle of corium and a little arcuate toward apex, feebly concavely angled at apex of corium. Connexivum moderately exposed and scarcely reflexed. Prosternum with a small tuberclelike elevation on either side of stridulatory groove. Mesosternum with a very prominent transverse fold or rounded carina. Venter roundly flattened near center. Legs of moderate length, the femora each with a small pair of tubercles subapically.

Color pale yellow above with black basal two antennal segments; antenniferous tubercles; sides of tylus and more or less extensive median line from base of tylus along vertex; line connecting eyes and ocelli, and ocelli and constricted neck region; lateral lines across bases of anterolateral tubercles and along lateral margins of pronotum, surrounding yellow lateral tubercles and extending a little onto lamellately expanded humeral margins; at middle of pronotum a longitudinal line which expands anteriorly to encircle anterior pair of yellow tubercles and proceeds backward laterally, encircling scarcely elevated smooth areas and terminating abruptly on either side at transverse impression; posteriorly divergent, scarcely elevated carinae of posterior lobe of pronotum; just lateral to each of these, a line which broadens and bends inward posteriorly and then bends abruptly outward on posterior margin to terminate just above basal angles of scutellum; a brief black line on sublateral longitudinal carinae; base, basal angles, sides of base of posterior prolongation, and median longitudinal, apically narrowing, depressed area and line reaching to depressed subapex of scutellum; sublateral vein of corium, particularly basally, as well as an arcuate longitudinal fascia at inner apical angle and an antemedian and postmedian zigzag transverse line and a small subapical area within sublateral vein; entire base of membrane along inner two-thirds of apical margin of corium and extending somewhat onto corium and veins of membrane, particularly on apical half; and anterolateral angles of connexival segments. Underside in great part black, with yellow acetabula and extensive areas on pleural plates, spiracles, and posterior two-thirds of each connexival segment. Legs ferruginous, the coxae black, the trochanters yellow to white, the femora yellowish basally and apically and blackish subbasally and subapically, tibiae black at bases and apices, tarsi piceous.

Female: Very similar to the male but larger. Proportion of antennal segments one to three, 23:62:60; fourth segment broken at middle.

Size.—Male: length 26 mm.; width (connexivum) 9 mm., (pronotum) 7½ mm. Female: length 29½ mm.; width (connexivum) 11 mm., (pronotum) 8½ mm.

Holotype, male, Barro Colorado, Canal Zone, Griswold Coll., in the Museum of Comparative Zoölogy, Harvard University. Allotype, female, Barro Colorado, Canal Zone, February 27, 1933, American Museum of Natural History.

Remarks.—Superficially resembling *Panstrongylus geniculatus* (Latr.), which likewise occurs on Barro Colorado Island, in general size and color, but actually very closely allied to *Mestor lignarius* (Walk.) from British Guiana. Mr. W. E. China has very kindly compared the male holotype with the type of *Conorhinus lignarius* Walker, a female, in the collection of the British Museum of Natural History. He writes: "At first sight your specimen appears to be identical with the unique type. Closer examination reveals the fact that it differs considerably in the structure and coloration of the pronotum and scutellum, particularly in the shape of the tubercles of the anterior lobe of the pronotum. The scutellum is also dark with a yellow median stripe in *lignarius* instead of yellow with a black median stripe as in your specimen. I have just found in our accessions another female specimen of *Mestor lignarius* collected in British Guiana in 1929. There is some slight variation in the

pronotal tubercles and coloration but in the main they are of the same pattern as in the type and quite distinct from your Panama specimen." As indicated above, the female specimen from Panama exhibits no appreciable variation except the usual sexual differences.

As Mr. China's excellent sketch of Walker's type shows, the entire anterior lobe of the pronotum behind the collar is black except for yellow lines from the anterior pair of tubercles to transverse impression. The posterior pair of tubercles is wanting, whereas the sublateral, scarcely elevated, smooth areas of *humeralis* are developed as distinct tubercles in *lignarius*. On the posterior lobe of the pronotum, the black markings of the posteriorly divergent carinae disappear behind the anterior fourth while the markings of the sublateral longitudinal carinae extend much farther forward and turn inward anteriorly. Also the apex of the scutellum is rounded rather than cordiform in *lignarius*.

Other related species are *Mestor rufotuberculatus* (Champion), which is clothed with pale, depressed hairs on the head, pronotum, and scutellum and has reddish pronotal tubercles and a subtriangular mesosternal elevation, and *Mestor megistus* (Burm.), which is much darker with reddish markings, has acute pronotal tubercles, and has a transverse but narrower, almost semicircular, thin, platelike elevation of the mesosternum.

Genus **Dipetalogaster** Usinger, n. gen.

Description.—Very large, polished, and naked except for short, scattered vestiture beneath and long hairs on appendages. Head twice as long as broad, eyes included; twice as deep at level of eyes as apically; anteocular region four times as long as postocular distance to posterior constriction. Eyes, seen from above, about half as broad as interocular space. Ocelli conspicuous, situated posterolaterally on oblique elevations. Antennae inserted a little before middle of anteocular region; very long, considerably surpassing distance from apex of head to apex of scutellum; first segment scarcely surpassing tip of head; second segment three times as long as first; third one-sixth longer than second; and fourth a little more than one-half as long as third; second segment remarkable in the possession of numerous very stiff, straight, slightly backwardly directed bristles, some of which are twice as long as diameter of the segment. Rostrum long and robust, second segment about as wide as diameter of front tibiae; first segment one-half the length of the second and a little more than one-third longer than the third.

Pronotum almost one-third broader behind than long on median line; one-third as broad anteriorly as posteriorly; anterior collar very distinct, the anterolateral angles bluntly, laterally produced; disk very coarsely rugose, with numerous sinuate, rounded elevations anteriorly but without distinct spines or tubercles; disk of posterior lobe very prominently elevated at middle, the sides subparallel posteriorly and humeral angles very broadly rounded.

Scutellum a little broader than long, roundly produced laterally at middle and elevated on lateral margins at middle; disk deeply rugose; posterior prolongation short and turned downward apically. Hemelytra rather short, scarcely surpassing base of sixth abdominal segment. Connexivum moderately dilated, the margins appearing double, owing to extension of ventral plates to abdominal margin. Legs very long, cylindrical, the femora with subapical paired-tubercles obsolescent.

Genotype, *Conorhinus maximus* Uhler (1894).

Remarks.—This genus is remarkable for its double-plated connexival margins, which immediately separate it from all other Triatomas known to me.

Such a condition is approached in the genus *Rhodnius,* where one also finds incipient postocular callosities suggestive of *Psammolestes.* The long bristles of the second antennal segment in *Dipetalogaster* are likewise found in *Triatoma chilena* n. sp., *Triatoma eratyrusiforme* Del Ponte, *Triatoma breyeri* Del Ponte, and perhaps in some other South American species.

Uhler's type, no. 24710, in the United States National Museum, is in a rather poor state of preservation. Larrousse (1924) has redescribed and figured the species. A third specimen (Cape St. Lucas, Albatross Expedition) is here recorded from the collection of the American Museum of Natural History. It is in perfect condition and has been used for the present study.

Genus *Triatoma* Laporte

The species of *Triatoma* present a great array of structural differences all of which are more or less modifications of the following: granulation or other peculiarities of body surface; vestiture of body and appendages, especially second antennal segment; form of head; place of insertion of antennae and proportion of segments; situation of ocelli; form and proportion of segments of rostrum; form and processes of pronotum; form and processes of scutellum, especially posterior prolongation; extent of ventral abdominal plates toward connexival margins; contour of ventral abdominal surface; form of female genital segments; and general coloration.

Although most of the species of *Triatoma* appear to be relatively stable, certain forms are much less distinct and seem to differ only in size, coloration, and other trifling details. Champion (1899), recognizing this, relegated Stål's *maculipennis* to a subspecific position within Latreille's species *dimidiata,* and Neiva (1911) found it necessary to separate the small Florida form of *sanguisuga* as a variety *ambigua.* It is my belief that such geographical isolates are of great significance biologically, especially in relation to the concept of general evolution. Hence, in accordance with present usage, I have employed the term subspecies to stand for the category represented by these forms.

Triatoma protracta (Uhler)

An exceedingly variable, widespread species of common occurrence in woodrats' nests (*Neotoma* spp.) throughout a great part of the western United States. I have seen specimens from California, Nevada, Utah, Colorado, New Mexico, Arizona, Texas, and Lower California. In Texas and New Mexico there occurs a smaller, smoother, and much paler form with a broadly margined connexivum, and certain specimens from Colorado and New Mexico are considerably larger, more unicolorous, and with the connexivum conspicuously larger and more dilated and the hemelytra somewhat abbreviated. The first of these forms has been collected in numbers sufficiently great to put its true status as a geographical subspecies seemingly beyond doubt. It is described below. Galliard (1935) has directed attention to two distinct types of eggs in his cultures of *protracta.* These are obvious in cultures from mixed

sources which are being studied in California at the present time. Rearing experiments may perhaps disclose two distinct species among our very variable California material. Differences, no matter how trivial or superficial they may appear, are perfectly sound and reliable if they reveal ecologically or genetically distinct forms.

Uhler's type material is to be found both at the California Academy of Sciences (two male paratypes, Monterey County, Calif., and one female paratype, Santa Clara County, Calif.) and at the United States National Museum, where the type number 24713 has been given to a specimen from San Diego, California.

Triatoma protracta subsp. woodi Usinger, n. subsp.

Description.—Closely allied to typical *protracta* from California, with the same short basal antennal segment, long basal rostral segment, thick hairy rostrum, rounded venter, and small eyes. At once distinguished, however, by its smaller size; smoother head, pronotal, and scutellar disks; short, scattered black hairs of pronotum and corium; and much paler, duller coloration, particularly on the hemelytra and abdomen, the connexivum being margined with testaceous.

Head more than twice as long as broad, 56::24; produced three times as far before the eyes as distance from posterior margins of eyes to posterior constriction; antenniferous tubercles terminating slightly more than one-third the distance from eyes to apex of head; disk roughened by numerous small, stiff hairs arising from small pits. Eyes very small; seen from above, only one-third as wide as interocular space. Antennae shorter than length of head and pronotum together, 17::20; proportion of segments one to four as 5:14:13:11. Rostrum stout, reaching to middle of prosternum, the ratio of segments one to three as 22:26:11; the third segment beset with long hairs. Pronotum a little shorter than head, 10::11; broader than long, 6::5; more than twice as broad at base as at apex, 12::5; anterior collar sharply defined; anterolateral angles scarcely produced, rounded; sides moderately sinuate and feebly carinate; anterior lobe with no trace of tubercles or spines; disk roughened by small pits anteriorly and short, stiff hairs posteriorly, and irregularly, feebly wrinkled throughout. Scutellum with posterior prolongation about one-third its total length, narrowed apically and distinctly turned downward at the tip. Venter evenly rounded.

Color fuscous, the apical antennal segments, neck, joints of rostrum and legs, hemelytra except at middle of corium and sometimes at apices, connexivum at least along margins above and below and sometimes much more broadly, pale ochraceous. The apex of clavus, inner apical portion of corium, and base of membrane hyaline. Membrane elsewhere light fuscous. Eyes black.

Size.—Male: length 15 mm.; width (pronotum) 3.5 mm., (connexivum) 4 mm. Female: length 16.2 mm.; width (pronotum) 3.5 mm., (connexivum) 3.75 mm.

Holotype, male, no. 4608, Mus. Calif. Acad. Sci., Ent., taken 13 miles west of Carrizoza, New Mexico, July 23, 1936, by S. F. Wood. Allotype, female no. 4609, Mus. Calif. Acad. Sci., Ent., same data as type. Paratypes, six specimens, same data as type; three specimens, Sunny Glen Ranch, Brewster County, Texas, May, 1926, 5000–7000 feet elevation, O. C. Poling (Iowa State College). Two specimens, Alamogordo, New Mexico, May 16, 1902 (Phila. Acad. Nat. Sci.). Other specimens before me which are too damaged to be included in the paratype series are the following: three specimens, same data as type; three specimens, 13 miles west of Las Lunas, New Mexico, July 29, 1936; four specimens, 54 miles east of Van Horn on U. S. Highway 80, Texas, July 18, 1936; and six specimens near Bosque, Bolito, Hudspeth County, Texas, July 17, 1936, all collected by S. F. Wood.

Remarks.—Attention should be directed to the exceedingly wide range of variation in the series of paratypes, the examples from Brewster County, Texas, being considerably paler with a fulvous ground color, more strongly

dilated posteriorly, and a little larger, 16–17 mm. This same paler general coloration is exhibited in the two specimens from Alamogordo, New Mexico, and a female from the type locality and another from Theodore, Texas, show the more strongly dilated connexivum. A specimen received from Dr. Cornelius B. Philip, collected by Vorhies and Taylor in the den of *Neotoma albigula,* Santa Rita Mountains, Arizona, is a little smaller and smoother than typical *protracta,* whereas other Arizona specimens are typical of *protracta.*

Triatoma nitida Usinger, n. sp.

Description.—A rather large species, with polished surface, large eyes, short scutellum, and sharply contrasting black and yellow coloration.

Head less than twice as long as broad (excluding constricted neck region), 63::36; surface very coarsely and irregularly rugose and pitted, with very obscure short hairs arising from some of the pits; produced more than twice as far in front of eyes as distance from posterior margins of eyes to posterior constriction, 33::14; tylus laterally swollen on basal half, the entire head distinctly transversely impressed at its base; interocular region evenly convex. Eyes a little less than half as broad, seen from above, as interocular space. Ocelli very prominent, situated posterolaterally on oblique, smooth elevations. Antennae inserted a little before middle of anteocular region; shorter than head and pronotum together, 129::145; first segment reaching almost to apex of head; proportion of segments one to four as 15:44:39:31. Rostrum very stout, the second segment wider than diameter of front tibiae at middle; proportion of segments one to three as 23:37:13; third segment beset with long, fulvous hairs. Pronotum almost one-fourth longer than head; one-fifth broader than long; more than twice as broad posteriorly as anteriorly, 5::2; disk unarmed; anterior lobe with a very deep pit posteriorly at middle; posterior disk with very large, smooth, irregular or subtransverse wrinkles; lateral margins carinate and a little reflexed except at humeral angles; anterolateral angles scarcely produced as rounded dilations. Scutellum broader than long, 9::8; the posterior prolongation a little more than one-third of total length, broad at base and tapering to subacute, downwardly turned apex. Corium rather smooth. Connexivum only moderately arcuate; finely, transversely rugose. Venter sharply, strongly flattened.

Color dark reddish brown to black, with ochraceous markings covering most of head above except along margins of juga, at base of tylus where a U-shaped fuscous mark is evident, interrupted transverse alternations on either side of middle of interocular space, and dark area between ocelli. Pronotum with ochraceous anterior and lateral margins and a loop on either side of middle of disk of anterior lobe. Each loop extending as a single line posteriorly on a longitudinal carina to level of transverse constriction; with an inner, smaller branch reaching to central, deep depression; and with a small Y-shaped mark extending from lateral margin just behind middle of anterior lobe, dilating inwardly and obliquely posteriorly. Humeral angles rather broadly ochraceous. Extreme tip of scutellum yellowish. Hemelytra entirely yellowish except for brown base of clavus, center of corium, and apex of corium except narrowly along margin, and dirty, infuscated or fumose membrane. Connexivum yellowish with a distinct, broad, black band transversely at middle of each segment above and below. Joints of appendages, apex of rostrum, and tarsi ochraceous.

Size.—Length 21 mm.; width (pronotum) 5.5 mm., (connexivum) 8 mm.

Holotype, male, Sabranetas, La Roja, Guatemala, in the Museum of Comparative Zoölogy. Paratype, La Ceiba, Honduras, June 5, 1916, taken at light by F. J. Dyer, in the collection of the United States National Museum. This last-named specimen bears the label "Triatoma inedita Neiva Ms." It is possible that Hase's record (1932) of *neotomae* from Venezuela refers to *nitida.*

Remarks.—*Nitida* is very close to *neotomae* Neiva, the type (no. 24711, U. S. Nat. Mus.) of which is from Brownsville, Texas. However, *neotomae* is

smaller, 17½ mm., with the disks of head and pronotum entirely brown, the venter only subflattened, and the last two antennal segments of equal length. The discal spot of the corium is relatively smaller in *neotomae* and the apical spot is not bordered with ochraceous.

Triatoma barberi Usinger, n. sp.

Description.—A species of moderate size, brownish coloration, finely granular surface, and moderately dilated, alternated connexivum.

Head twice as long (excluding constricted neck region) as broad, eyes included; produced almost three times as far in front of the eyes as behind to posterior constriction; surface beset with elevated pits; tylus parallel-sided at apex, strongly dilated and almost bulbous basally; disk of head strongly convex, particularly between the eyes, the ocelli inserted posterolaterally, midway between eyes and posterior constriction, on smooth, oblique elevations. Eyes relatively small; as seen from above, scarcely one-third the width of interocular space. Antennae inserted slightly more than one-third the distance from eyes to apex of head; shorter than length of head and pronotum together, 10::12; first segment not reaching apex of head; proportion of segments one to four as 14:40:24:23. Rostrum reaching middle of prosternum; very robust, the second segment about as thick as front tibiae; proportion of segments one to three as 25:31:12; sparsely beset with fine hairs, which are longest at apex. Pronotum unarmed; the elevated portions and margins finely granular; rest of disk coarsely, irregularly rugose with two posteriorly divergent, subcarinate elevations connecting anterior and posterior lobes; subequal in length to head on medial line; about one-fourth broader at humeral angles than long, 77::56; more than twice as broad posteriorly as anteriorly, 77::30; lateral margins distinctly but not sharply carinate throughout, sinuate; anterolateral angles produced as distinct, rounded tubercles. Scutellum a little broader at base than long, the posterior prolongation relatively short, scarcely more than one-third the total length, broad at its base and tapering to a downward-turned, rounded point posteriorly. Hemelytra not quite reaching tip of abdomen; corium finely granular and with a few larger, elevated granules; clavus and inner cell of corium apically submembranous. Venter rather evenly rounded.

Color rather uniformly brown throughout except for silvery eyes; ochraceous anterior portion of constricted neck region and very narrow elevated portion at extreme base of corium; fumose membrane and corium; pale tarsi; and reddish-ochraceous alternations of connexivum above and beneath. The connexival markings are transverse at the sutures of segments and extend over the entire basal half of each segment sublaterally. The last connexival segment is entirely pale in the male and brownish at base in the female.

Size.—Length 17.5 mm.; width (pronotum) 4 mm., (connexivum) 6.5 mm.

Holotype, male, no. 4610, Mus. Calif. Acad. Sci., Ent., Cuernavaca, Mexico, September, 1900. Allotype, female, no. 4611, Mus. Calif. Acad. Sci., Ent., Cuernavaca, Mexico, May, Barrett.

Remarks.—This distinct little species is dedicated to Mr. H. G. Barber. It superficially resembles *sanguisuga* and its allies, but these latter, as well as *indictiva* Neiva, have a more slender rostrum, larger eyes, a longer and more cylindrical head, and a long, subcylindrical posterior prolongation of the scutellum. *Heidemanni* Neiva is entirely covered with short, depressed black hairs; has larger eyes; and possesses a longer, subcylindrical posterior prolongation of the scutellum. *Barberi* is closest to *protracta,* which has a similarly formed, laterally carinate pronotum, a similarly granular and rugose surface, small eyes, a short, downwardly directed posterior prolongation of the scutellum, and similar hemelytra. *Protracta* is at once distinguished, however, by its concolorous connexivum and differently formed head.

Triatoma incrassata Usinger, n. sp.

Description.—A species of medium size, brownish coloration, finely granular surface, tremendously enlarged base of tylus, and pale-margined connexivum.

Head a little less than twice as long (exclusive of constricted neck region) as broad, eyes included, 51::29; produced less than three times as far before the eyes as distance from hind margins of eyes to posterior constriction; disk thickly beset with coarse, raised, pitted granules; tylus strongly swollen and even feebly roundly produced laterally at base near level of insertion of antennae; slender and decreasing in height anteriorly; interocular region roundly convex. Eyes, seen from above, a little more than one-third the width of interocular space. Ocelli situated posterolaterally on oblique elevations. Antennae inserted a little beyond basal third of anteocular region; shorter than head and pronotum together, 105::119; first segment not reaching apex of head; proportion of segments one to four 13:38:30:24. Rostrum stout, second segment a little thicker than front tibiae at middle; proportion of segments one to three as 24:27:11; beset with short, fine hairs becoming longer on apical segment. Pronotum a little longer than head on median line, 56::51; a little less than one-third broader behind than long, 75::56; one-half as broad anteriorly as posteriorly; disk unarmed but with the elevated ridges covered with coarse, pitted granules; posterior disk irregularly rugose; lateral margins distinctly but not sharply carinate, sinuate; anterolateral angles produced as distinct, rounded tubercles. Scutellum distinctly broader than long, the posterior prolongation only one-third the total length, broad at base, narrowed, rounded, and turned downward apically. Hemelytra not quite reaching apex of abdomen; corium slightly roughened, obscurely granular, and finely rugose; apex of inner cell of corium and apex of clavus membranous. Connexivum moderately and rather evenly arcuate. Venter evenly rounded.

Color rather uniformly brown, the antennae apically, neck, joints of legs, tarsi, and rostrum in part fuscotestaceous or lighter. Membrane fumose except near apex of corium, where it is hyaline. Yellowish ochraceous on narrow, elevated vein at extreme base of corium, and broadly along entire connexival margin above and beneath. Undersurface smooth, polished, and fulvous or paler.

Size.—Length 17.5 mm.; width (pronotum) 4 mm., (connexivum) 5.75 mm.

Holotype, male, no. 4612, Mus. Calif. Acad. Sci., Ent., Valley of Mexico, August, 1929, collected by Ynez Mexia.

Remarks.—Closely allied to *barberi*, from which it may be distinguished by its shorter head, larger eyes, strongly incrassate base of tylus, and marginal rather than alternated maculation of connexivum.

Triatoma chilena Usinger, n. sp.

Description.—Elongate, sides subparallel, beset with extremely long erect bristles on the body posteriorly beneath and on all parts of the appendages except first antennal segment. Body surface finely granular-rugose and polished.

Head more than twice as long as broad, eyes included, subcylindrical; anteocular region four times as long as postocular region to posterior constriction; tylus subbasally slightly enlarged; vertex transversely coarsely rugose throughout its length at middle. Eyes, seen from above, much broader than one-half width of interocular space. Ocelli large and situated posterolaterally on oblique elevations. Antennae inserted a little before middle of anteocular region; very long, their total length exceeding distance from apex of head to apex of clavus; first segment thickest, second more slender, third and fourth filiform and curved; first segment scarcely attaining apex of head, without hairs or bristles; second segment more than four times as long as first, densely beset with fine, erect, fulvous bristles about twice as long as diameter of segment, and with numerous erect black bristles almost five times as long as diameter of segment; vestiture of third and fourth segments more or less as in second segment; the third segment less than one-sixth shorter than second; and fourth

one-half the length of second. Rostrum reaching prosternum, the second segment about as wide as slender front tibiae; first segment less than half as long as second; third one-fourth as long as second; sparsely, irregularly pilose, especially apically, and with a few long bristles at base. Pronotum two-thirds as long as broad behind and one-third as broad anteriorly as posteriorly; anterolateral angles produced laterally as bluntly pointed tubercles; disk unarmed, strongly convex, all but obscuring the transverse impression, which is represented merely by the feebly depressed posterior margins of callosities; callosities with broad, minutely granular, vermiform areas; longitudinal carinae only feebly elevated above the general convexity; disk sublaterally depressed, the humeral angles rounded. Propleura produced ventrally just before front coxal cavities and on either side of prosternal stridulatory groove as blunt, rounded tubercles. Scutellum much broader than long, subtriangular, produced posteriorly as a very short, subacute, upturned tubercle; disk roughened but unarmed. Hemelytra very long, the membranes distinctly surpassing tip of abdomen. Connexivum scarcely dilated, reflexed. Venter, in the specimens before me, sublaterally depressed and appearing longitudinally roundly keel-like at center; with long, suberect, backward-directed bristles posteriorly. Legs very long and slender, bearing long black bristles; the femora without short tubercles or spines beneath.

Color brownish with a trace of piceous on the head and maculated areas of ventral surface of abdomen. Elsewhere on venter dark brown to ferruginous. Eyes silvery, ocelli white. Connexivum alternated with reddish yellow about the sutures of segments. Tarsi, joints of appendages, and sutures in general pale.

Size.—Length 19 mm.; width (pronotum) 4 mm., (connexivum) 5 mm.

Holotype, male, Cruz Grande, Province of Coquimbo, Chile, November 9, 1916, T. Hallinan, accession number 5385, American Museum of Natural History. Paratype, male, same locality as type, November 25, 1916, in my collection.

The paratype differs only in that the hemelytra are slightly longer, the total length of the insect, in consequence, approaching 21 mm.

Remarks.—*Chilena* is readily distinguished from other Triatomas by its convex pronotum and short, triangular scutellum suggestive of *Cavernicola*, the long bristles of the second antennal segment suggestive of *Dipetalogaster*, and its elongate, slender form.

The recently described *Triatoma spinolai* Porter (1933) might possibly be confused with *chilena,* as it is of approximately the same size and was collected in the same province. In *spinolai,* however, the second antennal segment bears very short hairs and the connexivum is uniformly red. From the measurements given (width of pronotum 5 mm., of connexivum 6 mm.) this species must be more robust than *chilena.*

Triatoma rubrofasciata (Degeer)

This species, the type of the genus, is widely distributed throughout the warmer portions of both hemispheres. Kirkaldy (1904b) believed that it originally came from Brazil and that it reached the Hawaiian Islands by way of California. In this he was most certainly in error, for the species is mostly confined to coastal regions in America and is entirely absent in western North America, the records for this area and Mexico being based upon various forms of *Triatoma rubida* (Uhler). Neiva's belief that the original home was India appears to be much more plausible and the species seems structurally more closely allied to other Old World species than to any American species known to me.

The records of *rubrofasciata* from the United States as listed in most catalogues are based upon misidentifications, with the possible exception of the two records of Walker (1873) from Missouri and East Florida. Neiva examined 130 specimens of this species in many of the principal museums of Europe and America and found none from within the borders of the United States. It is of interest, then, to record a male and a female which are typical *rubrofasciata* from this country. They bear the label, "Jacksonville, Florida. April 8. Ac. 26226, Collection of Mrs. A. T. Slosson," and are preserved in the collection of the American Museum of Natural History.

Triatoma picturata Usinger, n. sp.

Description.—Very large species with abdomen strongly dilated and color predominantly ochraceous above. Dorsal surface beset with short, dark, stiff, subdepressed hairs.

Head more than twice as long as broad, eyes included; subcylindrical, being thickest a little behind the eyes, where it is slightly dorsally elevated; tylus very long, slender apically and a little dilated basally; anteocular portion three times as long as postocular portion to posterior constriction; vertex with a longitudinal line along middle, composed of about four rows of unusually dense, subdepressed black hairs and bounded on either side by a naked area. Eyes, seen from above, scarcely broader than one-half the width of the interocular space. Ocelli very large and prominent, situated posterolaterally on oblique, rounded elevations. Antennae inserted almost at middle of anteocular region; equal in length to distance from apex of head to apical third of scutellum; first segment slightly exceeding apex of head; proportion of segments one to four as 38:93:68:43. Rostrum reaching onto prosternum; fairly stout, the second segment a little narrower than diameter of front tibia; proportion of segments one to three as 21:31:10; erect hairs on apical segment. Pronotum a little shorter than head on median line; distinctly broader behind than long, 13½::10; and one-third as broad anteriorly as posteriorly; anterolateral angles produced as subacute, stout, sublaterally directed spines; lateral margins feebly carinate posteriorly; posterolateral angles subrounded; disk with a pair of prominent, subacute tubercles just in front of middle and another on the margins just behind middle; posterior lobe feebly and smoothly elevated centrally. Scutellum about as long as broad; posterior prolongation a little more than one-third total length, cylindrical and only slightly turned upward apically. Hemelytra rather long, reaching at least to middle of last abdominal segment. Abdomen very strongly dilated, exposing the entire connexivum as well as portions of abdominal disk on either side of hemelytra. Venter rather smoothly rounded, the entire undersurface clothed with long, fine, posteriorly directed hairs.

Color black except for ochraceous dorsal disk and pleura of posterior lobe of pronotum, the black extending onto posterior disk along longitudinal carinae; broad basal, narrow marginal, and broad subapical ochraceous areas of coria; entire connexivum above and beneath except for black areas on anterior half of each segment laterally; ochraceous posterior one-eighth of discal abdominal segments above; and subtriangular ochraceous areas at sutures laterally on ventral plates. The neck, apex of rostrum, apical two antennal segments, apex of scutellum, and tarsi pale. Eyes silvery.

Size.—Male: Length 32½ mm.; width (pronotum) 7 mm., (connexivum) 14 mm. Female: Length 34 mm.; width (pronotum) 7 mm., (connexivum) 15½ mm.

Holotype, male, no. 4613, Mus. Calif. Acad. Sci., Ent., Vic. Compostela, Nayarit, Mexico, December 10, 1933. Allotype, female, no. 4614, Mus. Calif. Acad. Sci., Ent., same locality as type, August 5, 1933. Paratypes, two males, same locality as type, April 22, 1933, and June 1–7, 1934, all from the collection of the University of California through the courtesy of Dr. W. B. Herms; one male, Nayarit, Mexico, December 1, 1933, in my own collection; and one specimen from Tepic, Nayarit, Mexico, in the collection of the United States National Museum.

Remarks.—Three nymphs of fourth or fifth instar are at hand from the type series. They vary from 23 to 28 millimeters in length and from 10 to 15½ millimeters in width at middle of abdomen. The connexivum is strikingly alternated with black on the anterior half and reddish ochraceous on the posterior half of each segment. The posterolateral angles of the narrow pronotum are distinctly though bluntly produced.

This species is very close to *phyllosoma* Burmeister, specimens of which are before me from more central and southern localities in Mexico. *Phyllosoma* differs in its much darker coloration, which includes an entirely black pronotum; the very long, erect hairs of the dorsal surface; the less elevated, rugose disk of posterior lobe of pronotum; and the short hemelytra. *Picturata* is one of the largest and most strikingly çolored species of *Triatoma* as yet described. I know it only from the state of Nayarit.

Triatoma longipennis Usinger, n. sp.

Description.—A large species with strongly dilated abdomen; short, scattered, subdepressed black hairs on upper surface; and convex central disk of posterior lobe of pronotum.

Head, including constricted neck region, more than twice as long as broad, eyes included; anteocular portion three times as long as distance from posterior margins of eyes to posterior constriction; disk scarcely elevated, reaching highest point just behind the eyes; tylus subbasally dilated; vertex with two sublateral, longitudinal, naked lines. Eyes, seen from above, scarcely wider than one-half interocular space. Ocelli very large and conspicuous, situated on posterolateral, oblique elevations. Antennae inserted very slightly behind middle of anteocular region; first segment just reaching apex of head; proportion of segments one to three, 28:75:59 (fourth segment broken off). Rostrum reaching prosternum; relatively slender, the second segment not so wide as diameter of front tibia; proportion of segments one to three as 36:56:19; apical segment with long, curved, fulvous hairs. Pronotum as long on median line as head (excluding the neck); more than one-fourth broader behind than long; and three times as broad posteriorly as anteriorly; anterolateral angles produced into sublaterally directed, subacute tubercles; disk of anterior lobe with two prominent, subacute tubercles a little before middle and two less prominent ones at lateral margins just behind middle; posterior disk centrally rather strongly elevated and smoothly convex; lateral margins carinate; and humeral angles briefly produced and subrounded. Scutellum longer than broad; posterior prolongation almost as long as the remaining portion and strongly turned upward posteriorly. Hemelytra long, nearly reaching to tip of abdomen. Connexivum broadly dilated and reflexed. Venter smoothly rounded; covered with short, subdepressed brown hairs; the long, fine, black hairs so characteristic of the entire surface of *phyllosoma* being largely confined, in *longipennis*, to the mesosternum.

Color dark ferruginous to black. Disk of the posterior lobe of pronotum ferruginous, becoming fulvous to yellowish sublaterally. Venter ferruginous. Apical antennal segments, ocelli, tarsi, joints and apex of rostrum, and joints of legs pale. Eyes silvery. Entire basal fifth of corium and a subapical spot which does not reach lateral margin, reddish ochraceous. Connexivum with posterolateral angles of segments broadly, subtriangularly, reddish ochraceous above and beneath, the last abdominal segment with margins entirely reddish ochraceous except for a short distance on either side at base.

Size.—Length 29 mm.; width (pronotum) 6.75 mm., (connexivum reflexed) 10 mm.

Holotype, male, no. 4615, Mus. Calif. Acad. Sci., Ent., collected at Venedio, Mazatlan, Mexico, on July 27, 1918, by J. A. Kusche and presented to the California Academy of Sciences by B. Preston Clark. Further specimens from northwestern Mexico are in the United States National Museum.

Remarks.—This appears to be the species figured by Champion as *phyllosoma* (1899). From our present incomplete knowledge of its distribution it appears to be confined to northwestern Mexico. *Phyllosoma,* of which I have both sexes from central and southern Mexico, may easily be distinguished by its more strongly constricted pronotum, with a flatter and more rugose posterior disk; its very long, curved, black hairs on almost the entire body surface; and its abbreviated hemelytra, which reach only to the middle of the fifth visible abdominal segment in my specimens.

The records of *phyllosoma* have been confused, owing to a lack of precise definition of the various species concerned. Thus, as shown above, it appears likely that Champion's *phyllosoma* from northwestern Mexico is *longipennis* n. sp. Furthermore, it seems likely that Uhler's "dark variety" from San Diego (1876) was, in fact, Barber's recently described *longipes* (1937b), which occurs near by in Arizona.

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EXPLANATION OF PLATE

MEALYBUGS AND THEIR INSECT ENEMIES
IN SOUTH AMERICA

BY

HAROLD COMPERE

CONTENTS

MEALYBUGS AND THEIR INSECT ENEMIES IN SOUTH AMERICA

BY

HAROLD COMPERE

PART I: TAXONOMIC STUDIES—NEW ENCYRTIDAE PARASITIC IN MEALYBUGS

INTRODUCTION

IN PART I of this paper five species of mealybug-inhabiting Encyrtidae are described as new and four species previously described are noticed.

The species of *Anagyrus* reared from mealybugs in South America remain mostly undetermined. Many of them cannot be identified until the species of the group are classified. A large number of *Anagyrus* species can be said to be named only. Many have been described without regard to previously named species. The descriptions are inadequate, lacking any mention of the characters by which closely related species can be separated. In one group are ten or fifteen named species, none of which can be differentiated on the basis of the published descriptions. The species of *Aenasius* collected in South America are reported upon in a paper published in the Proceedings of the Hawaiian Entomological Society.[1]

LEPTOMASTIX DACTYLOPII Howard
(Fig. 1)
Leptomastix dactylopii Howard, U.S.D.A., Bur. Ent. Bul., 5:23, 1885.

Leptomastix dactylopii was described by L. O. Howard from specimens reared in 1884 from *Pseudococcus citri* (Risso), infesting *Paeonia* on the grounds of the Department of Agriculture, Washington, D. C. Howard stated that the mealybug infestation was completely destroyed by this parasite. Later he reported that *L. dactylopii* had been collected on the Island of St. Vincent in the British West Indies in 1894. In the collection of the Citrus Experiment Station is a series of specimens determined as *L. dactylopii*, reared from *P. citri* on figs, taken by W. E. Bradley at Baton Rouge, Louisiana, October, 1923. *L. dactylopii* is now established in California from specimens imported from Brazil.

The California stock of *Leptomastix dactylopii* was propagated from a single pair which issued December 24, 1934, from *Pseudococcus citri*. The parasitized mealybugs were collected in a nursery, "Floricultura Fluminense," at Nictheroy, Estado Rio de Janeiro, December 12, 1934, where they infested *Cassia splendens* and chayotes. The material was shipped to Riverside by air express. The two *L. dactylopii*, reared at Riverside by Flanders, were permitted to mate, after which the female was liberated in a cage con-

[1] The species of *Aenasius*, encyrtid parasites of mealybugs, Proc. Haw. Ent. Soc., 9(3): 383–404, 1937.

taining a quantity of *P. citri* growing on potato sprouts. In less than three weeks, her progeny began to issue. By the end of 1935 more than four million individuals of *L dactylopii*, each a descendant of the single pair imported from Brazil, had been propagated in the insectaries and released in the orchards of California.

The specimens of *Leptomastix dactylopii* which have been studied taxonomically are not in exact agreement with Howard's original description, because of color differences Howard stated that his specimens showed considerable variation in color, and this is also true in regard to ours. The species can be identified from the following brief description and figure 1
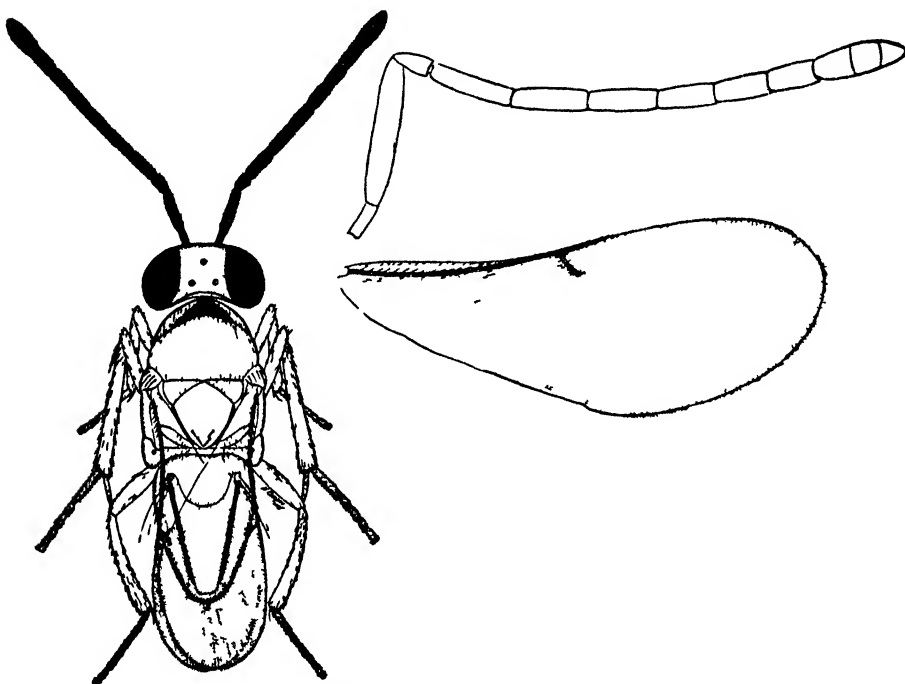
Fig. 1. *Leptomastix dactylopii* Howard. Female

Female.—Honey yellow to brownish yellow with the following dark brown to blackish markings antennae except the ventral part of the scape, occiput widely across the middle; concealed part of the pronotum; mesosternum; narrowly on the vertical edges on the sides of axillae and scutellum. Sides of propodeum and the abdomen in parts, more or less brownish or fuscous. Tarsi faintly dusky.

Male—Colored similarly to the female except for more extensive blackish markings. Abdomen often completely blackish; collar of pronotum and anterior margin of mesoscutum narrowly blackish.

In life both females and males hold the wings semierect so that they extend at an angle of about 45° to the longitudinal axis of the body.[3]

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[3] Biological note by S. E. Flanders. *Leptomastix dactylopii* is an active, hardy parasite which reproduces freely in the insectaries. Its preferred hosts are the larger-sized mealybugs. Only one individual can complete its development in a single host. The life cycle is completed in thirteen days at a temperature of approximately 80° F. The feeding period of the larva is about four days. There are five larval instars.

LEPTOMASTIX BAHIENSIS n. sp.

This species can be distinguished by the white antennal club and the narrow, oblique, infuscated crossband on the forewings.

Female.—Dominantly testaceous to whitish, the abdomen partly brown to fuscous. Frontovertex yellow; face and cheeks mostly white. Sides and underparts of the thorax anterior to the mesopleura and the tegulae whitish; mesopleura testaceous. Abdomen suffused with fuscous on the sides toward the apex; yellowish white on the sides toward the base, at the extreme apex, and across the base: whitish ventrally; brown centrally on the dorsum. Scape longitudinally broadly streaked with white, the dorsal and ventral sides and the radical joint blackish; pedicel pale at apex; funicle entirely blackish; club white. Legs white to yellowish, with the dorsal margin of the middle femora longitudinally brownish and the middle and hind tibiae toward the base narrowly streaked with brownish. Forewings with a blackish to brown band extending diagonally inward from the costa part way across the blade; the crossband about as wide as the length of the stigmal vein, its inner margin parallel to the outer margin of the speculum, and its end at a distance less than its own width from the posterior margin of the blade. The blade on either side of the crossband with fine, refractive cilia; basal part of the wing partly infuscated. The infuscated area with coarse, fuscous cilia. Hind wings with a central crossband of transparent, refractive cilia.

Head, vertical position dorsal aspect, a trifle more than twice as wide as long; frontovertex more than one-third the head width (5:13); ocelli in an actue triangle, the posterior pair about one-half their diameter from the orbits and two diameters from the occipital margin. Frontovertex appearing granular, the granular effect produced by close, shallow punctations. Head, frontal view, as wide as high; scorbes almost vertical, not meeting above; the median convexity of the face between the scorbes visible in profile. Antennae inserted about midway between the orbits and the oral margin. Anterior to the ocelli, the setae hardly visible on the frontovertex except for the row paralleling each orbit.

Scape slightly less than one-third as wide as long, narrowly expanded ventrally, widest toward the apex. Pedicel about twice as long as wide and plainly more than one-half as long as the first funicle joint. Funicle joints all successively decreasing in length; the first about three times as long as wide; the sixth slightly longer than wide (4:3). Club slightly longer than the preceding two funicle joints.

Postmarginal vein about twice as long as the stigmal vein; marginal vein with a hyaline break basad of the speculum.

Sides of mesoscutum narrowly reflexed and explanate, a character not present or slightly developed in the other species available for study.

Length, 1.5 mm.

Described from 6 females, holotype and paratypes, reared by H. Compere from *Ferrisana virgatus* (Ckll.), infesting *Macquilla tomentosa*, São Salvador, Bahía, Brazil, October, 1934.

LEPTOMASTIDEA ABNORMIS (Girault)

Paraleptomastix abnormis Girault, Entom., 48:184, 1915.
Tanaomastix abnormis Timberlake, Univ. Calif. Publ. Entom., 1:362, 1918.
Leptomastidea abnormis Mercet, Bol. Real Soc. Esp. Hist. Nat., 24:4, 1924.

A few specimens of this species were reared from *Pseudococcus citri* (Risso) collected at Nictheroy, Estado do Rio de Janeiro, Brazil, December, 1934.

TETRACNEMUS PEREGRINUS n. sp.
(Fig. 2)

This is the fourth species to be assigned to Westwood's genus *Tetracnemus*. The type species, *T. diversicornis* Westwood, is known only from the original

description and the figure of a male showing the branched antennae. The illustration of the type species shows the axillae as widely separated. The species subsequently described have the axillae meeting or almost meeting. *T. brounii* was described by Timberlake in a comparative way with regard to *T. pretiosus*, and the latter species was fully described. This new species is described relative to *T. pretiosus* and, unless otherwise mentioned or figured, it is in close agreement with all the characters mentioned by Timberlake in his description of *T. pretiosus*. The female of the new species can be distinguished readily from *T. pretiosus* and *T. brounii* by the relatively short first funicle joint.
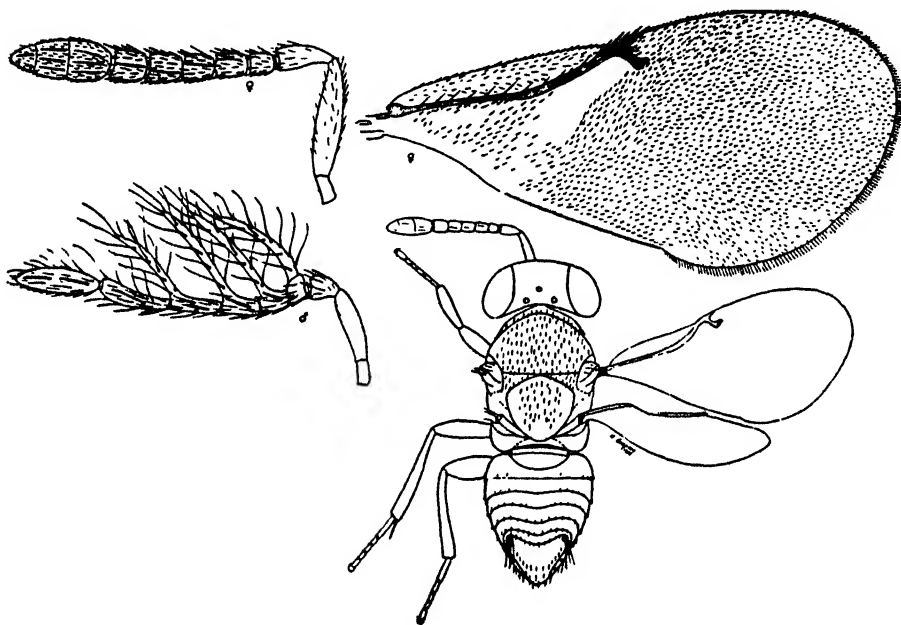
Fig. 2. *Tetracnemus peregrinus* n. sp. Female with detached wing and antenna. Male, antenna.

Female.—Dominantly blackish to dark brown, with faint bluish green reflections on the head and mesoscutum, and with fainter bronzy reflections on the scutellum; scrobes highly refringent, with reddish purple reflections. Scape testaceous on the basal half or so, the remainder of the antennae dark brown or blackish. Legs mostly pale yellowish brown, with the hind coxae, most of the hind femora, and usually a slight blotch on the hind tibiae near the base slightly fuscous to brown.

Ocelli in a right triangle. Antennae, as shown in figure 2; first funicle joint the shortest, hardly longer than wide; in the other species the first funicle joint about three times as long as wide. Forewings, as shown in figure 2, clear, hyaline, the basal part of the blade with a pattern of coarse dark cilia; postmarginal vein short but distinct. Sculpture less distinct than in *Tetracnemus pretiosus*, possibly because of the much smaller size.

Length, 0.8 mm. to 1.0 mm.

Male.—The male of the new species does not differ appreciably from *Tetracnemus pretiosus* except for the more uniform dark brown to piceous color and a more extensive pattern of cilia on the basal part of the forewings, which is about like that of the female shown in the figure. In *T. pretiosus* the speculum is margined on the proximal side by two or three

rows of cilia, and most of the basal part of the blade is bare except for cilia crowded beneath the submarginal vein and a projection which partly cuts off the speculum from the bare posterior margin.

Length, 0.8 mm. to 1.0 mm.

Described from 15 females and 23 males, holotype, allotype, and paratypes, as follows: 13 females and 22 males reared from *Pseudococcus longispinus* (Targ.), collected by H. Compere at Rio de Janeiro, Brazil, in August and September, 1934; 2 females and 1 male reared at Riverside by S. E. Flanders from material imported from Buenos Aires, Argentina, where it was collected by H. Compere in March, 1935.

In the collection of the Citrus Experiment Station is a series of specimens reared from material imported from Cape Town, South Africa, in 1924, where it was collected by E. W. Rust. Another small series of specimens was received in 1926 from F. W. Petty, who reared them from a mealybug on pears at Elsenburg, Cape Colony, South Africa.

This species was exceedingly abundant on ferns infested with mealybugs in the patio of the American Embassy at Rio de Janeiro in September and October, 1934. Several shipments of parasitized mealybugs were sent to California. Flanders reported rearing 375 adult *Tetracnemus* from the imported material. Colonies were liberated in several orchards, and an attempt was made to propagate the species in the insectary at Riverside. Dissections of parasitized mealybugs showed that the species is a primary parasite. The larvae are of the same type as those of *T. pretiosus*.

WATERSTONIA Mercet

Waterstonia Mercet, Bol. Real Soc. Esp. Hist. Nat., 17:268, 1917. Eos, 1(1): 18–19, 1925.

In Mercet's key to *Aphycus* and related genera the new species *diversicolor* runs to *Waterstonia* because of these characters: mandibles acute, tridentate, the median tooth the largest; maxillary palpi four-jointed; labial palpi three-jointed; ovipositor shortly exserted and flexible, enclosed by the ventrites almost to the apex of abdomen; antennae uniformly pallid; marginal vein punctiform; funicle six-segmented. It does not agree with the species of *Waterstonia* previously described, which have the dorsum of the thorax with white appressed setae. In *diversicolor* the mesoscutum and scutellum have fine, brown setae. Except for the mandibles, which are tridentate instead of bidentate, this species looks much as if it were congeneric with *Cirrhencyrtus ehrhorni* Timberlake. The principal difference between the genus *Waterstonia* Mercet and *Cirrhencyrtus* Timberlake seems to be the mandibles, which are tridentate in *Waterstonia* and bidentate in *Cirrhencyrtus*.

KEY TO THE SPECIES OF WATERSTONIA

1. Forewings with two transverse, infuscated bands. Dorsum of thorax with white, appressed pubescence.. 2
   Forewings with an infuscated area on the anterior part of the blade centered beneath the marginal vein. Mesoscutum and scutellum with fine, dark setae. Abdomen with a broad, brownish black band across the middle, the base whitish, the apex yellowish. Dorsum of head, axillae, scutellum, and mesopleura orange-yellow: mesoscutum lemon-yellow. Ovipositor exserted about one-fifth the length of the abdomen. Posterior ocelli about once their own diameter from the orbits.................[Brazil] *diversicolor* n. sp.

2. Ovipositor exserted about one-third or one-half the length of the abdomen........... 3
    Ovipositor exserted about one-fourth or one-fifth the length of the abdomen. Abdomen
      dark brown, yellow at base, rounded at apex. Mesoscutum, axillae, and scutellum yellow.
      Posterior ocelli more than once their own diameter from the orbits..................
                                                            [Spain] *secunda* Mercet
3. Abdomen reddish with the borders dark brown, truncate at apex. Mesoscutum, axillae,
      and scutellum reddish yellow. Ovipositor exserted about one-half the length of the
      abdomen. Posterior ocelli once their own diameter from the orbits..................
                                                              [Spain] *prima* Mercet
    Abdomen with a broad, brownish black band across the center, the base and apex bright
      orange-yellow. Ovipositor exserted about one-third the length of the abdomen. Posterior
      ocelli about one-half their own diameter from the orbits.............................
                                                  [United States] *bifasciata* (Timberlake)

Waterstonia diversicolor n. sp.

Female.—Concealed part of pronotum and abdomen widely brownish black across the
middle. Dorsum of head, axillae, scutellum, and mesopleura orange-yellow. Base of abdomen
white. Other parts grading from light lemon-yellow to whitish. Center of forewings with
a large infuscated spot extending about halfway across the blade beneath the marginal vein.

Dorsum of head convex; frontovertex finely punctate, two and one-half times as long as
wide; ocelli in an acute angle, the posterior pair about once their own diameter from the
orbits and nearly twice as far from the occipital margin. Head in frontal view about as
wide as high; the frontovertex narrowly descending beneath the inner basal corners of
the eyes; scrobes well defined, semicircular above, reaching upward well beyond the basal
ocular line.

Scape long and slender, at least five times as long as wide. Pedicel two and one-half times
as long as wide. First funicle joint slightly wider than long, the succeeding increasing in
size, the sixth about one and one-half times as wide as long. Club wider than the funicle
and almost three times as long as wide.

Length, 1.1 mm.

Male.—Similar to the female except that most of the propodeum, metanotum, wing proc-
esses, and more of the pronotum are blackish.

Described from 3 females and 6 males, holotype, allotype, and paratypes, reared from
a *Pseudococcus* sp., questionably *nipae*, taken on bamboo palm at Santos, Brazil, by
H. Compere, November 2, 1934.

Ericydnus clavicornis n. sp.
(Fig. 3)

This species agrees generically with Mercet's diagnosis of *Ericydnus* Walker
except as follows: funicle joints all wider than long; pedicel almost as long
as the first three funicle joints united; club large, almost as long as the pedicel
and funicle joints united. Axillae slightly separated at the inner ends. Meso-
scutum, axillae, and scutellum with fine, dark setae instead of white setae.
Costal cell of hind wings wide. Basal abdominal segment not differentiated
from those following by either color or sculpture.

Female.—Frontovertex dark bluish green merging to blackish on the face and cheeks.
Dorsum of thorax mostly shining bluish black with violaceous reflections; the mesoscutum
appears a trifle more bluish than the axillae and scutellum, the latter the most violaceous;
remainder of the body and the head black. Scape brown in sharp contrast to the remainder
of the antennae, which is black. All tarsi except the distal ends and the distal ends of all
tibiae brown, the rest of the legs blackish. Forewings very faintly infuscated distad of the
speculum.

Head, normal position dorsal view, menisciform, four times as wide as long; frontovertex
about one-fourth the width of the head; ocelli in a trifle less than a right angle, the posterior

pair almost touching the orbits and almost once their own diameter from the occiput. Fronto-vertex with umbilicate punctations in addition to fine reticulations; the punctures descend anteriorly between the scrobes and orbits, but fade out before reaching the genal sulci. Head, in frontal view, wider than high (5:4); eyes long, descending three-fourths the depth of head; antennae inserted about a socket's length from the mouth; scrobal impression rounded above and reaching upward well above the basal ocular line. Mesoscutum convex; scutellum large, almost plane, pointed at apex; axillae slightly separated. Abdomen in dry, tag-mounted specimens triangular, acute at apex, shorter than the thorax.

Antennae eleven-jointed, exclusive of a large asymmetrical ring joint furnished with several setae. Scape slender, with a ventral longitudinal excavation on the distal half. Pedicel
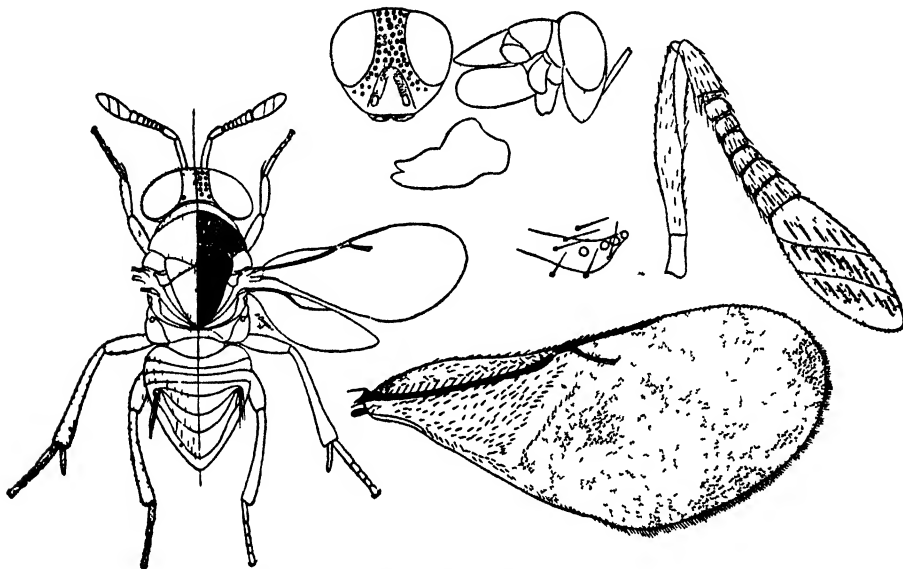
Fig. 3. *Ericydnus clavicornis* n. sp. Female.

fully twice as long as wide and as long as the first three funicle joints united. All funicle joints wider than long, gradually increasing in size, the first slightly wider than long, the sixth twice as wide as long. Club large, at least one and one half times as wide as the sixth funicle joint and almost as long as the pedicel and funicle joints united. Mandibles with two well-developed teeth. Maxillary palpi four jointed; labial palpi three-jointed. Fore-wings large, very closely and finely ciliated distad of the speculum; marginal fringe short; marginal vein about twice as long as wide; postmarginal vein very long, more than one-half as long as the submarginal vein; stigmal vein long but only about one-half as long as the postmarginal vein, not much widened at apex.

Mesoscutum, axillae, and scutellum punctate reticulate and furnished with fine, short, dark setae.

Length, 2.0 mm.

Described from 8 females, holotype and paratypes, reared by Edson Hambleton as follows: 4 from *Pseudococcus* sp. (Hambleton's no. 5), taken at Jacutingo, Sul de Minas Geraes, and 4 from *Pseudococcus* sp. (Hambleton's No. 8), taken at São Paulo, Brazil, in January, 1935.

METAPHYCUS ALBOCLAVATUS n. sp.

Female.—Scape, basal half or more of the pedicel and first two or three funicle joints black to dark brown, remainder of antennae white. Dorsum of head, mesoscutum, axillae, and scutellum orange-yellow, in some lights mesoscutum with slight golden reflections. Col-

lar of pronotum silvery white. Tegulae white with a faint dusky spot. Metanotum and most of propodeum blackish. Abdomen mostly dark brown, paler toward the apex. Face and cheeks yellow with traces of dusky most pronounced above the mouth. Wings hyaline and without a band of paler-colored cilia. Head, thorax, and abdomen with short, appressed white setae.

Scape slightly expanded, three times as long as wide. Pedicel twice as long as wide. First four funicle joints much the smallest, short, transverse; the fifth and sixth much larger, the sixth almost twice as wide as long. Club about twice as long as wide and almost as long as the funicle, the sutures very faint so that the club might easily be mistaken as being solid. Mandibles with three subequal blunt teeth. Maxillary palpi four-jointed, the apical joint fuscous in contrast to the preceding; labial palpi three-jointed. Head in frontal view about as wide as high, the cheeks occupying less than one-half the depth. Frontovertex two and one-half times as long as wide; occipital margin rounded. Ocelli in an acute triangle, the posterior pair about one-half their diameter from the eye margins and twice their diameter from the occipital margin. Postmarginal vein spurlike, no longer than the marginal vein. Speculum almost reaching the posterior margin of the wing, slightly separated from the basal hairless area by fine, faint cilia. Tibial spur of middle legs about one-half as long as the basitarsus. Ovipositor rigid, long, rising near base of abdomen and shortly exserted; not enclosed by ventrites toward the apex.

Length, 1.0 mm.

Described from 5 females, holotype and paratypes, reared from an undetermined *Pseudococcus* sp. by Edson Hambleton at São Paulo, Brazil, in January and February, 1935. Hambleton's no. 8.

AENASIUS ADVENA Compere

Aenasius advena Compere, Proc. Haw. Ent. Soc., 9(3):393, 1937.

This species was described from a series of specimens reared from *Ferrisana virgatus* (Ckll.), collected by Swezey on the Island of Oahu, Territory of Hawaii, in 1934.

A single female collected by the writer in October, 1934, at São Salvador, Bahía, Brazil, appears to be specifically the same as *Acnasius advena*, described from specimens collected in Hawaii. In the Brazilian specimen, the scape is completely black, the first three funicle joints testaceous, and the sides and underparts of the thorax are brownish black.

ANAGYRUS PSEUDOCOCCI (Girault)
(Fig. 4)

Epidinocarsis pseudococci Girault, Entom., 48(627):185, 1915.
Anagyrus pseudococci Timberlake, Proc. Haw. Ent. Soc., 8(1):158–159, 1932.

This species was described from specimens reared from *Pseudococcus citri* (Risso), collected by H. J. Quayle in Sicily in 1913. Some specimens of the lot obtained by Quayle in Sicily are in the collection of the Citrus Experiment Station. The determination of the South American specimens as *Anagyrus pseudococci* is based on a comparative study of these samples.

Anagyrus pseudococci was obtained in large numbers from *Pseudococcus citri* (Risso) on various host plants in the city of Buenos Aires, Argentina. Two shipments of *P. citri* parasitized by *A. pseudococci* were sent to California. This material, collected in Parque Lezica and in the patio of a private dwelling, Las Heras Avenue, Buenos Aires, produced three hundred and

twenty-nine adults after its arrival at Riverside. *A. pseudococci* was success-
fully propagated by S. E. Flanders on *P. citri* in the quarantine room. Colo-
nies were liberated in several orchards and others supplied to local insectaries.[a]
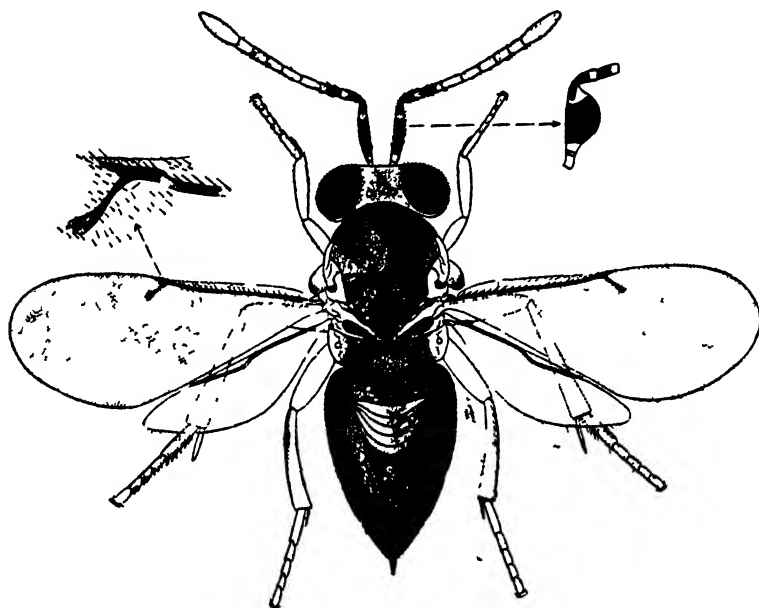
Fig. 4. *Anagyrus pseudococci* (Girault). Female.

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[a] Biological note by S. E. Flanders. *Anagyrus pseudococci* did not reproduce readily when
confined in cages. The egg hatches within forty-four hours after deposition; the larval feed-
ing period is about five days. The host becomes "mummified" on the seventh day after receiv-
ing the parasite's egg. At a temperature of about 78° F the life cycle is completed in
eighteen days. *Pseudococcus citri* reacts strongly to the presence of the parasitic egg. A
large, irregular, melanized, cellular mass accumulates about the egg. The larva may be able
to maintain an opening in this matrix if the egg hatches before the material becomes too
dense.

In the shipments from Argentina, the fully developed larva of *Anagyrus pseudococci*
were parasitized by the immature males of *Coccophagus heteropneusticus* Compere.

Part II. Some South American Mealybugs, with Notice of Their Insect Enemies

INTRODUCTION

The observations recorded here and the collection and shipment of insect enemies of mealybugs from South America to California were made incidental to an investigation of the red scale, *Chrysomphalus aurantii* (Mask.). In the South American exploration by the University of California Citrus Experiment Station, assistance was received from the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture. Traveling expenses were met from a fund contributed by the citrus growers of California. The entire project was under the supervision of Professor Harry S. Smith, the exploration and collections being made by Harold Compere, and the imported beneficial species cared for by S. E. Flanders upon their arrival at the insectary of the Citrus Experiment Station.

Special attention was paid to those species of mealybugs which occur in both California and South America, so that the most useful mealybug-feeding species from South America might be introduced into California. The mealybugs of economic importance occurring in both California and South America to which special attention was given are: *Pseudococcus maritimus* (Ehrh.), *Pseudococcus citri* (Risso), *Pseudococcus longispinus* (Targ.), *Pseudococcus gahani* Green, and *Phenacoccus gossypii* (Towns. and Ckll.).[4]

An attempt was made to introduce and establish in California all the South American beneficial species which appeared likely to prove of value here. Eleven of the shipments of beneficial insects sent from South America contained some parasites or predators of mealybugs for trial in California. Six of the mealybug-feeding species obtained from the South American shipments were propagated in the insectary at Riverside. At least one of these species, *Leptomastix dactylopii* Howard, is now established in California. Although its host, *Pseudococcus citri* (Risso), is of minor importance as a citrus pest, occasionally *P. citri* occurs in sufficient numbers, in certain areas of Ventura and San Diego counties, to be injurious to citrus crops. *Leptomastix dactylopii* gives promise of being of appreciable economic value.

PSEUDOCOCCUS COMSTOCKI (Kuwana)
(Pl. 2)

Pseudoccocus comstocki (Kuwana) is the mealybug commonly found on citrus in Brazil, and not *Pseudococcus citri* (Risso) as reported in the litera-

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[4] The greater number of mealybug species collected in South America remain undetermined. Some of them have been reported upon by Edson Hambleton, Archivos do Instituto Biologico, São Paulo, 6(13):105–120(1935). No attempt has been made to obtain determinations of some coccinellids of the genera *Nephus, Diomus, Hyperaspis, Eriopsis*, or of other miscellaneous predators such as syrphid flies, cecidomyids, and lacewings. Only a part of the mealybug-inhabiting chalcidoids collected in South America are reported upon in Part I of this paper.

ture. In most of the citrus orchards visited in the Federal District and in the states of Rio de Janeiro and São Paulo, *P. comstocki* was seen. Only rarely was this mealybug abundant enough to be rated as injurious. In Argentina scattered specimens of *P. comstocki* were noticed on citrus in the province of Misiones. Several small but exceedingly injurious infestations were discovered on citrus trees grown for shade and ornament along the sidewalks of city streets in Asuncion, Paraguay.

In habits, appearance in life, and morphologically the South American species determined as *Pseudococcus comstocki* appears to be similar to the Asiatic species, which is commonly found on citrus in China and Japan.[5] When infesting citrus trees, the colonies of *P. comstocki* appear distinctive. The individuals tend to congregate in small, compact colonies which are sheltered between adhering leaves, within the folds of curled leaves, and between fruits that are touching. Plate 2, supplied through the courtesy of Edson Hambleton, of the Instituto Biologico, is an excellent likeness of this common but little-known citrus-infesting mealybug.

No evidence of chalcidoids parasitic in *Pseudococcus comstocki* was noticed in Brazil, although predators of various kinds were seen feeding upon it. In Asuncion, Paraguay, remains of old infestations were abundant in some localities, and great masses of mealybug detritus containing "mummies" with parasite exit holes were present, but none of the parasites were obtained.

PSEUDOCOCCUS CITRI (Risso)

Pseudococcus citri (Risso) was noticed in most of the South American countries visited. This species, which freely attacks citrus in many parts of the world, was rarely found on citrus in Brazil, but was noticed frequently on other host plants. Several small but injurious infestations were discovered. In the Brazilian publications dealing with citrus insects, *P. citri* is figured correctly, but it is not, as alleged, the common citrus-infesting species. Two species of Encyrtidae, *Leptomastidea abnormis* (Girault) and *Leptomastix dactylopii* Howard, were reared from *P. citri* in Brazil. The first of these species was introduced into California from Sicily in 1913, and the second was established in California from stock imported from Brazil in 1935. Numerous predators feed upon *P. citri* in Brazil, including *Hyperaspis c.-nigrum* Mulsant, *Nephus* sp., *Diomus* sp., species of lacewings, and cecidomyids.

In Argentina, *Pseudococcus citri* is generally distributed in the city and environs of Buenos Aires, where it infests various ornamental plants. It was commonly noticed on oleanders in small colonies mixed with *Pseudococcus longispinus* (Targ.). Generally the infestations of *P. citri* were not heavy enough to be injurious. An exception to this was an infestation on an isolated citrus tree growing in the patio of a dwelling. The tree had been defoliated and mealybug egg masses hung in festoons from the limbs. Chalcidoid parasites and various predators were abundant. *Anagyrus pseudococci* (Girault),

[5] For a discussion of the identity of the Asiatic species, see the Canadian Entomologist, 65:243–245, 1933.

which was propagated and colonized in California, was obtained from material collected here.

Pseudococcus citri is a pest of major importance in Central Chile, where it injuriously infests many different kinds of ornamental and food plants. It was also noticed in abundance on oleanders at Lima, Peru. In these two countries there was no evidence of internal parasites, and the few predators present did not appear to be of appreciable value.

PSEUDOCOCCUS LONGISPINUS (Targioni)

Pseudococcus longispinus (Targ.) was first collected in Brazil on ferns growing in pots in the open-air patio of the American Embassy at Rio de Janeiro. This find was of interest to Brazilian entomologists, as *longispinus* was not supposed to occur in that country. Subsequently, it was found that *Pseudococcus longispinus* was generally distributed in Brazil and that it was occasionally abundant and injurious to various kinds of ornamental plants in dooryard gardens. When the infestation was discovered in the patio of the Embassy, it had passed the peak of abundance. Large masses of mealybug detritus adhered to the dead fronds. These masses contained countless mummified mealybugs, some containing mature larvae and pupae, others being merely empty shells with parasite exit holes. *Tetracnemus peregrinus* Compere was ovipositing in the live mealybugs which congregated on the new shoots and few remaining live fronds. Dissections of the live mealybugs showed that nearly all of them contained eggs or larvae of this parasite. *T. peregrinus* attacks the very small mealybugs. In some of the gardens in the city of Rio de Janeiro, occasional mature *Pseudococcus longispinus* were noticed which had been mummified by the action of some large internal parasite. In Argentina, *Pseudococcus longispinus* is rather common on ornamental plants. In the city of Buenos Aires it was often noticed on oleanders. In Central Chile this mealybug is abundant and injurious enough to be classed as a serious pest.

PHENACOCCUS GOSSYPII (Townsend and Cockerell)

Phenacoccus gossypii (Towns. and Ckll.) is now coming into prominence as a pest of ornamental plants in California. In Brazil it was first found on tomato vines at Nictheroy, and a few days later additional specimens were taken on hedge plants in the city of Rio de Janeiro.

The discovery of these few specimens led to a special search for the purpose of obtaining parasites of *Phenacoccus gossypii* for introduction into California. One isolated but exceedingly injurious infestation was found on hollyhocks in the compound of the Rio de Janeiro Light and Power Company. Some of the most heavily infested plants had been killed to the ground, the leaves being brown and withered and covered with mealybug detritus. Other plants retained a few green leaves which were covered with mealybugs. Near-by *Coleus* and chrysanthemums were infested and an adjoining brick wall was white with ovipositing mealybugs and old egg masses. Numerous predators of various kinds were feeding on the mealybugs, including coccinellids of the

genera *Hyperaspis, Diomus,* and *Nephus,* dipterons of the genera *Leucopis* and *Diplosis,* and syrphid flies and lacewings. There was no evidence of internal parasites, nor were any reared from material sent to Riverside.

Although a special lookout was kept for *Phenacoccus gossypii* in São Paulo, it was not found by the writer. Its presence there has recently been reported by Edson Hambleton, who is continuing the search for parasites that might be of value in its control in California.

PSEUDOCOCCUS MARITIMUS (Ehrhorn)

Pseudococcus maritimus (Ehrh.) was discovered on ornamental plants in three different gardens in the city of São Paulo. This discovery was of local interest, as this mealybug was not supposed to occur in Brazil. Altogether, hardly more than a dozen plants were infested. There were no signs of inter-

Fig. 5. *Hyperaspis c-nigrum* Mulsant.

nal parasites, but predators were abundant, including species of *Hyperaspis, Nephus, Diomus, Eriopsis, Diplosis, Leucopis,* and *Chrysopa.* These infestations almost disappeared while under observation by the writer during November, 1934, and a few months later Hambleton reported that it was impossible to find live mealybugs. The disappearance of these localized heavy infestations is attributed to the work of predators.

The most common and effective of these predators appeared to be *Hyperaspis c-nigrum* Mulsant (fig. 5), a coccinellid that feeds upon various species of mealybugs in Brazil. This is one of the beneficial insects introduced into California. Although no internal parasites were noticed attacking *Pseudococcus maritimus* in Brazil, Flanders succeeded in getting *Acnasius paulistus* Compere to reproduce in this host. *Pseudococcus maritimus* was not noticed in Argentina by the writer, but, according to Lizer Trelles, it is probably the same as the species which is a pest of grapes and known there as *Pseudococcus vitis* (Nied.). In Chile, *Pseudococcus maritimus* ranks as a pest of major importance and injuriously infests a variety of fruit and ornamental trees.

PSEUDOCOCCUS GAHANI (Green)

Pseudococcus gahani (Green) is the most injurious and abundant of the mealybugs which attack cultivated plants in Chile. In that country the mealybugs are pests of first rank. Four species of *Pseudococcus* are involved—

gahani, citri, longispinus, and *maritimus.* The infestations are often composed of two or more species. In the famous agricultural valley of Quillota, growers stated that at least one-third of their crop of avocados and cherimoyas was destroyed annually by mealybugs. Here the growers scrape the ovipositing females and egg masses away and scrub the tree trunks in an effort to prevent mealybug injury. In Los Leones, the fashionable residence district of Santiago, sidewalks under the shade trees were black and sticky with excrement from mealybugs overhead. In shops of Santiago, *Pseudococcus gahani* were noticed crawling in show windows where infested fruits were offered for sale. Injurious infestations were seen in orchards, dooryard gardens, cemeteries, plazas, and along public streets. In Central Chile, mealybugs are common and conspicuous enough to have attracted the notice of the general public, and have been aptly named "chanchitos blancos"—little white pigs.

SUMMARY

So far as biological control is concerned, the mealybug situation in South America is extremely interesting. It is quite possible that the mealybug fauna of Brazil will eventually prove to be one of the richest in the world. Prior to the collections of Hambleton and the writer, hardly more than twelve species of mealybugs were known from Brazil. Hambleton has now collected between forty and fifty species on cultivated plants in the gardens of São Paulo and adjacent towns. Because of their relative unimportance in Brazil, the mealybugs in that country have received but slight attention. This paper and one published by Hambleton record for the first time the occurrence in Brazil of four species of mealybugs which are internationally known as serious pests. The general noninjuriousness of these well-known cosmopolitan species in Brazil, as well as the noninjurious character of many of the endemic species, is to be attributed in large measure to the work of predators and parasites. In marked contrast, however, to the mealybug conditions in Brazil is the situation in Central Chile, where the endemic coccid fauna is meager. Only four species of mealybugs were noticed there. These four species are not native to Chile, but presumably were accidentally introduced through the importation of infested nursery stock. All four species are common and occur in injurious numbers. No effective insect enemies of mealybugs, either native or introduced, were noticed in Chile. The introduction of parasitic and predacious enemies of mealybugs into Chile presents one of the most attractive biological projects of today. The exploitation of the numerous parasitic and predacious species that occur in Brazil has only commenced.

EXPLANATION OF PLATE

PLATE 2

Pseudococcus comstocki (Kuwana). (After Hambleton.)

THE INSECT ENEMIES OF THE
BLACK SCALE, SAISSETIA OLEAE (BERN.)
IN SOUTH AMERICA

BY

HAROLD COMPERE

CONTENTS

THE BLACK SCALE, SAISSETIA OLEAE (BERN.), IN SOUTH AMERICA

BY

HAROLD COMPERE

INTRODUCTION

THE COLLECTION of insect enemies of the black scale, *Saissetia oleae* (Bern.), in South America and their shipment to California was incidental to an investigation of red scale, *Aonidiella aurantii* (Mask.). The South American exploration for enemies of the red scale was undertaken by the University of California Citrus Experiment Station. The salary of the explorer was paid by the University of California, and the traveling expenses from a fund raised by the organized citrus industry. Approximately one year was spent in South America by the writer on this project. The beneficial insects sent to California were cared for by S. E. Flanders at the insectary of the Citrus Experiment Station at Riverside. The entire project was under the direction of Professor Harry S. Smith, in charge of beneficial-insect investigations.

THE STATUS OF THE BLACK SCALE IN SOUTH AMERICA

The early history of the black scale, *Saissetia oleae* (Bern.), in South America is not known. The scale is believed not to be native to that continent. Possibly it was accidentally imported from Africa on infested nursery stock. The earliest record of black scale in South America is by Adolph Hempel, who listed it as occurring in São Paulo, Brazil, in 1898. In recent South American entomological publications, the black scale is mentioned as occurring in Brazil, Argentina, Chile, and Peru.

In Brazil black scale was found in nearly all the localities visited, but in the tropical countries it was never or rarely on plants which it commonly infests injuriously in temperate regions. Much citrus was examined in tropical orchards and gardens, and only once was any found with more than a few black scale scattered here and there. The exception was a sparse infestation on the trunks and main branches of young orange trees at Bom Retiro, São Gonçalo, Estado do Rio de Janeiro. In general the plants favored by black scale in temperate climates, oleanders, cycads, olives, *Euonymus,* and citrus were not infested in Brazil. The commonest and most favored hosts of black scale in Brazil are *Cassia splendens* and *C. imperialis,* two ornamental trees indigenous to Brazil and commonly planted along streets and sidewalks and in parks and gardens.

In Brazil, injurious infestations of black scale were rarely found, although a few scales were usually present on many cassia trees. The worst infestations were discovered in places not readily accessible to insects, usually on scattered, isolated trees in the densely built industrial and business sections of the cities.

The most destructive infestation of black scale discovered in Brazil was

found at Nictheroy in October, 1934. For a distance of several miles along Rua Marquez do Paraná, a main thoroughfare, most of the young cassia trees were heavily infested. Black scales in all stages were present: the leaves were covered with crawlers, and the branches were encrusted with "rubber sized" and adult scales. There was little evidence of parasitism when the infestation was first discovered. As the season advanced, parasites became increasingly numerous and their work more evident. By the end of January, 1935, the infestation had subsided, and it was no longer possible to obtain parasitized scales for shipment to California. The abundance of adult parasites which eventually developed and the large proportion of scales with parasite exit holes were indications that parasites had caused the reduction of this infestation. The infestation along Rua Marquez do Paraná was not unique except in size. Heavily infested individual trees were found in four different out-of-the-way places in the city of Rio de Janeiro. These infestations also declined after the parasites increased to large numbers.

In the state of Bahía, black scale was found on cassia trees in the cities of São Salvador and Alagoinhas. In São Salvador a few trunk sprouts on old cassia trees were found lightly infested, and in Alagoinhas a single cassia pod was found encrusted with immature, parasitized black scale. Although many citrus trees were inspected in this region, they appeared to be free of black scale. At Santos, black scale on cassia trees along a main street showed no evidence of parasitism. On the Brazilian Plateau in the state of São Paulo, explorations were made in the cities of São Paulo, Campinas, and Limeira, and their vicinities. Here, where the climate is more temperate and where one would expect to find black scale abundant, there were fewer than in the more tropical parts of Brazil. In this region the only infestation worth mentioning was on a vine, *Ficus repens,* growing over a masonry wall in a back yard. The scales were confined to three or four square yards of matted vine. All were of small size and appeared to be stunted. A large proportion of the very small scales had been parasitized, the exit holes remaining as evidence. This material produced *Euaphycus* sp., a black scale parasite not found elsewhere. At Fazenda Sete Quedas, near Campinas, a few scattered, dead black scales were found on citrus in the orchard. Near a dwelling was found a slight infestation of live black scale on *Cassia imperialis,* nearly all of which were inhabited by the larvae of *Lecaniobius utilis* n. sp. and *Scutellista cyanea* Motsch. In the city of Campinas, two cassia trees were found lightly infested with parasitized black scale. At Limeira, where extensive citrus plantations exist, only isolated, old black scales were noticed.

The observations in Argentina were very limited. In Buenos Aires, black scale attacks oleanders even more freely than it does in California. This is in marked contrast to the situation in Brazil, where black scale rarely or never infests oleanders. In Palermo Park, Buenos Aires, a few citrus trees were lightly infested with live black scales, and a good proportion of the *Cycas revoluta* scattered in gardens and parks had a few scales. Nearly all the black scales on oleanders, regardless of size, were brown and dry, appearing as

though "cooked." A record high temperature for Buenos Aires was recorded early in February, 1935, when the thermometer stood at 105° F. a few weeks before these observations were made. Live black scales which contained parasites were found in several moist, shady places. In one public park near a lagoon, where the grass land was soggy with moisture, oleander branches were on the ground and covered with mud deposited by Argentine ants. The mud-covered parts of the branches in contact with the ground were encrusted with live black scale. In La Plata, black scale was found in small numbers on the same host plants which it usually infests in California. In Misiones, in northeastern Argentina, where the climate tends to be tropical, black scale was not found in the citrus orchards, but it did occur on two species of ornamental plants. In the dry, temperate climate of Mendoza in western Argentina, where grapes, olives, and deciduous fruits are grown, black scale is reported to be a pest of olive trees. Here considerable quantities of old shells were found on oleanders, and the leaves were crowded with very young scales. Very few of the old scales had parasite exit holes.

In Chile, black scale is far more injurious than in any other country of South America. There it infests the same kinds of plants, with but few exceptions, that it infests in California. Avocados are more freely attacked than in California. The most injurious infestations were on shade trees along streets of Vina Del Mar, near Valparaiso. The black scale in Chile is not parasitized; at least, no exit holes were noticed, except where colonies of parasites recently imported from California had become established.

In Peru, black scale was noticed on oleanders at Lima and Choiseca. It appeared to be of little or no importance there.

THE INSECT ENEMIES OF BLACK SCALE IN SOUTH AMERICA

In 1916, Girault described *Aneristus oculatipennis* from two specimens reared by Rust, in 1912, from *Saissetia oleae* (Bern.), at Catacaos, Peru. In 1933, Fonseca and Autuori recorded *Scutellista cyanea* Motsch. from *Saissetia oleae* in Brazil. The writer has described[a] *Aneristus brasiliensis* from specimens reared by Edson Hambleton from *Saissetia olcae* collected at Viscosa, Minas Geraes, Brazil, 1933. These records give the information relative to the insect enemies of the black scale in South America acquired prior to this report.

The chalcidoid parasites in the following list were reared from *Saissetia oleae* in South America in the fall of 1934 and spring of 1935:

1. *Scutellista cyanea* Motsch. Brazil, Argentina
2. *Lecaniobius utilis* n. sp. Brazil, Argentina
3. *Coccophagus heteropneusticus* n. sp. Brazil, Argentina
4. *Coccophagus fallax* n. sp. Brazil
5. *Coccophagus lycimnia* Walker. Brazil
6. *Coccophagus basalis* n. sp. Brazil
7. *Aneristus brasiliensis* Compere. Brazil
8. *Aneristus oculatipennis* Girault. Brazil

[a] H. Compere, Notes on the classification of the Aphelinidae, Univ. Calif. Publ. Entom., 6(12):287, 1936.

9. *Aneristus pallidiceps* n. sp. Brazil
10. *Tomocera* sp. Brazil
11. *Euaphycus* sp. Brazil
12. *Encyrtus* sp. Brazil
13. *Gahaniella saissetiae* Timb. Brazil
14. *Eupelmus coccidivorus* Gahan. Brazil
15. *Eupelmus?* sp. Brazil
16. *Eurytoma?* sp. Brazil

In addition to the chalcidoid parasites listed above, a cecidomyid belonging to *Diplosis,* or a closely allied genus, and two coccinellids of the genus *Azya* were obtained from black scale in Brazil.

Some of the chalcidoids in the list are injurious hyperparasites, and others are primaries of slight or no economic importance. Without much doubt, *Gahaniella saissetiae* Timb. and *Eupelmus coccidivorus* Gahan belong to the former category. Likewise, the unidentified species of the family Eupelmidae and Eurytomidae are suspected to be hyperparasitic in black scale. The undetermined species of *Encyrtus* may have issued from *Saissetia hemisphaerica* (Targ.) accidentally mixed with the black scale that were unnoticed at the time. Regardless of its exact host relations, the *Encyrtus* sp. was rare, and only two specimens were obtained. The undetermined species of *Euaphycus* was found in one locality only. At the time of its discovery, live parasites were exceedingly rare. An appreciable percentage of the very small black scales were empty shells with exit holes indicating that previously *Euaphycus* sp. had been fairly abundant. *Coccophagus fallax* n. sp. probably was the most numerous and most frequently reared of the black scale parasites taken in Brazil. No effort was made to propagate this species and colonize it in California, because of a mistake in its identity.

Another common parasite of black scale in Brazil which was not successfully propagated in the insectary at Riverside is *Aneristus brasiliensis* Compere. This species was repeatedly reared at Riverside from black scale imported from Brazil, but efforts to obtain reproduction in cages in the quarantine room all ended in failure. Flanders succeeded in getting *Aneristus pallidiceps* n. sp. to produce a few specimens of a second generation in the quarantine room, but this species eventually died out. Both *Aneristus pallidiceps* n. sp. and *Aneristus oculatipennis* Girault were rare in Brazil and were found only at São Salvador, Bahia, a decidedly tropical region. *Coccophagus basalis* n. sp., which rather rarely parasitizes young black scale in Brazil, did not succeed in reproducing in the quarantine room at Riverside.

It is thought that the two most valuable of the South American black scale parasites have been obtained. These two species, *Lecaniobius utilis* n. sp. and *Coccophagus heteropneusticus* n. sp., were the only species except *Scutellista cyanea* Motsch. which ranged from tropical and subtropical Brazil into temperate Argentina. The failure to find the other Brazilian black scale parasites in temperate Argentina, where the temperatures are comparable to those in southern California, may be significant. In Buenos Aires, where the winter temperatures are comparable to those at Los Angeles, California, the work

of *Coccophagus heteropneusticus* n. sp. was very commonly seen. In the old black scales the work of this parasite is readily identified. It is the only South American species which leaves small, multiple exit holes in the old shells. A large proportion of the old black scales noticed on *Cycas revoluta* in the city of Buenos Aires were marked with from two to five or six small exit holes. Because of the similarity of the work of *Scutellista cyanea* and *Lecaniobius utilis*, it was not possible to estimate the relative abundance of these two species. The records kept of the rearings made from South American material in the quarantine room at Riverside show that *Scutellista* was more abundant than *Lecaniobius* in the material received. In December, 1935, *Lecaniobius utilis* was recovered from an orchard in Ventura County, California, where some of the first liberations were made. *Coccophagus heteropneusticus* has not been recovered from the orchards in California.

One of the species of *Azya* found feeding on black scale in Brazil readily reproduced in the insectary and is established in at least one orchard in Ventura County, where some of the first liberations were made. A cecidomyid found working on black scale at Rio de Janeiro was not propagated at Riverside.

Seventeen shipments of beneficial insects were made from South America to California: fourteen from Brazil, and three from Argentina. Thirteen of the shipments contained some parasitized black scales.

The types of the new species described in this article are to be deposited in the United States Museum, and paratypes in museums of the South American countries where the specimens were collected.

1. *Scutellista cyanea* Motschulsky

Scutellista cyanea Motschulsky, Etud. Entom., 8:171, 1859.

Scutellista cyanea is supposed to be native to Africa. Its presence in South America is very likely the result of an importation of nursery stock infested by a coccid in which *Scutellista* were living. Since *Scutellista* already occurs in California, no attempt was made to propagate or colonize specimens received from Brazil. It was interesting to note that *Scutellista* was just about as effective an enemy of black scale in the tropical climate of Rio de Janeiro as it is in the temperate or subtropical regions in California, Africa, and Australia. The insectary records show that 690 live *Scutellista* were reared from South American material received at the insectary of the Citrus Experiment Station, and that, in addition to those counted, an uncounted number were destroyed or allowed to perish.

2. *Lecaniobius utilis* n. sp.

(Figs. 1, 2)

According to A. B. Gahan, this species is undescribed and is similar in many ways to his species *capitatus*, but it may be distinguished at once by the uniformly ciliated basal part of the forewings. The other described species

of *Lecaniobius* is *cockerelli* Ashmead. The three described forms may be sep-
arated by the following key:

1. Head in frontal view only slightly wider than high (5:4); the raised area between the
     scrobes and orbits of almost uniform width from near the base of the scrobes to the
     anterior ocellus above...2
   Head in frontal view one and one-half times as wide as high; the raised area between
     the scrobes and orbits much narrowed below. The forewings beneath the marginal vein
     clouded with golden refractive cilia. British West Indies, Florida..*cockerelli* Ashmead
2. Base of the forewings with an elongate patch of dense, dark cilia extending obliquely
     distad and caudad from the base of the submarginal vein but terminating before reach-
     ing the transverse band. Panama................................*capitatus* Gahan
   Base of the forewings generally ciliated except narrowly along the posterior margin.
     Brazil, Argentina...*utilis* Compere n. sp.

Female.—Dark metallic with strong bluish and violaceous reflections. The vertex, temples,
pronotum, and anterior, dorsal corners of the mesopleura strongly bluish. Axillae and meso-
sternum greenish blue. Scutellum dark brown, opaque. Prepectus and tegulae black, opaque.
Most of head below the eyes ferruginous, the antennal scape concolorous. Basal part of
abdomen on the dorsum and the arched apex of the seventh tergite translucent, brownish,
or colorless. Ovipositor sheaths pale straw-colored. Knees of fore and hind legs more or
less dark brown. All tarsi dark brown. Middle tibiae with a colorless translucent blotch on
the flattened, anterior apical angle. Most of head on the dorsum and the mesoscutum with
violaceous and bluish reflections blended.

Conspicuous, silvery white, refractive pubescence arranged as follows: A wide dense
band on the mesopleura extending diagonally from near the fore coxae toward the base
of the forewings; anterior and posterior margins of the hind coxae on the outer aspect;
lateral angles of the propodeum; axillae adjacent to the scutellum, apex of scutellum; sides
of the mesoscutar lateral lobes; mesosternum and ventral part of the mesopleura; abdomen
except most of the dorsum; most of head. On the raised area between the scrobes the silvery
setae are flattened, larger, and appear more conspicuous than similar setae on the cheeks,
which are in less contrast against the ferruginous coloration. Most of the mesoscutum
except the crests of the two lateral ridges rather sparsely covered with fine, silvery white
setae. Scutellum with a median longitudinal row of coarse, short, black setae.

Sculpture mostly finely and closely punctate-reticulate. On the outer sides of the lateral
lobes the reticulations are more striate than punctate. On the axillae, close to the scutellum,
the punctations are slightly larger. Scutellum with short, close, longitudinal reticulations.
Exposed parts of the prepectus with close, deep reticulations that produce a scalelike effect.
The sculpture of the head is varied: punctate on the frons and transversely reticulated on
the vertex.

Forewings as shown in figure 1. Beneath the marginal vein the cilia are coarse, dense, and
fuscous, giving the wing the appearance of having a broad median infuscated band sep-
arated by a hyaline streak from a triangular basal area set with similar setae. The hyaline
streak is furnished with fine, silvery, refractive cilia. The postmarginal and stigmal veins
are obscured beneath the dense clothing of fuscous cilia.

Length of average-size samples, 3.0 mm.

Male.—Color dark blue-black blended with greenish and violaceous. The mesoscutum
and scutellum slightly less brilliantly metallic. Frontal part of head dominantly bluish or
greenish. Most of thorax, abdomen, and legs dominantly violaceous, except the tarsi, which
are mostly white; apical tarsal joints dusky; spur of middle tibiae white; paired spurs of
hind tibiae fuscous; knees of all legs more or less faintly brownish; anterior apical margin
of middle tibiae with a trace of whitish. Radical joint of antennae ferruginous, the flagellum
opaque, blackish.

The silvery pubescence is sparse and usually scattered, only the propodeum conspicuously
pubescent; face and cheeks with rather inconspicuous squamous setae.

The sculpture on parts of the head and mesoscutum less coarsely and less extensively punctate-reticulate than in the females.

Head, in dorsal view, twice as wide as long, the frontovertex occupying one-half the width. Ocelli almost in a transverse line, the posterior margin of the anterior ocellus tangent to an imaginary line traversing the anterior margins of the posterior ocelli. Occipital margin rounded. Head, in frontal view, almost as high as wide; eyes moderately small, protuberant, hardly longer than the width of the cheeks. Antennal sockets widely spaced, tangent to the basal ocular line. Scrobes wider, shorter, and more divergent than in the female, rounded above, deeply excavated, the margins carinated. As in the female, the area between the
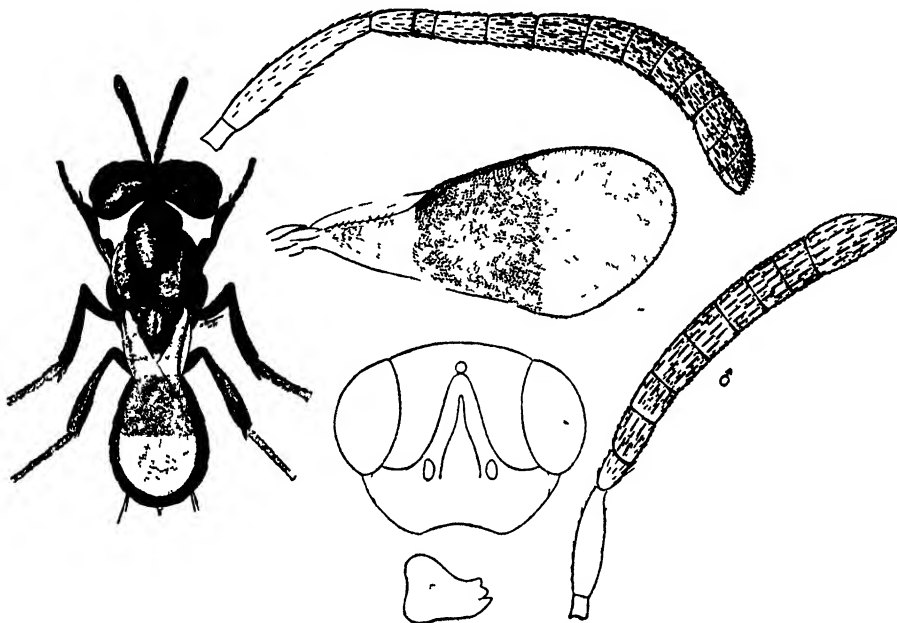
Fig. 1.—*Lecaniobius utilis* n. sp. Female: entire insect and detached antenna, wing, frontal aspect of head, mandible. Male: antenna.

scrobes and orbits more elevated than the interscrobal plane. Anterior ocellus placed just above the margin of the scrobal impressions.

Thorax strongly convex; axillae steeply declivous, prepectus, viewed laterally, triangular in shape, with the apex near the insertion of the forewings. On the mesoscutum a slight break in the uniformity of the curvature indicates the parapsidal furrows. Abdomen much smaller than the thorax, spatulate in shape.

Club and funicle hardly differentiated, the flagellum of almost uniform width throughout. Pedicel small, slightly longer than wide; funicle joints slightly decreasing in length distad, the first four plainly longer than wide. Antennae as shown in figure 1.

Forewings broad with moderately sparse, fine, white cilia. Wing veins white. Marginal vein plainly shorter than the submarginal vein. Postmarginal vein plainly longer than the stigmal vein and fully one-half as long as the marginal vein.

Length, 2.0 mm.

Described from 55 females and 6 males, holotype, allotype, and paratypes, propagated at Riverside on *Saissetia oleae* (Bern.), in 1935, or collected in different localities in Brazil and at Buenos Aires in Argentina, September, 1934, to March, 1935.

Samples of this species were reared from *Saissetia oleae* by Edson Hambleton at Viscosa, Minas Geraes, Brazil, in May and August, 1933. Two poorly preserved specimens are in the collection of the Citrus Experiment Station

with the California State Insectary number 1070. The insectary records show that these specimens were reared by George Compere from *Saissetia oleae* at Bahia, Brazil, in 1904, and that they carried his number 1528. In the records of George Compere is the entry, "1528—Black-scale parasites of Brazil. Few specimens liberated in West Australia."

The insectary records of the Citrus Experiment Station show that 151 live *Lecaniobius utilis* were reared at Riverside from material imported from South America. This species was collected at Rio de Janeiro, Nictheroy, Bom Retiro, and Campinas, in Brazil, and at Buenos Aires, in Argentina.
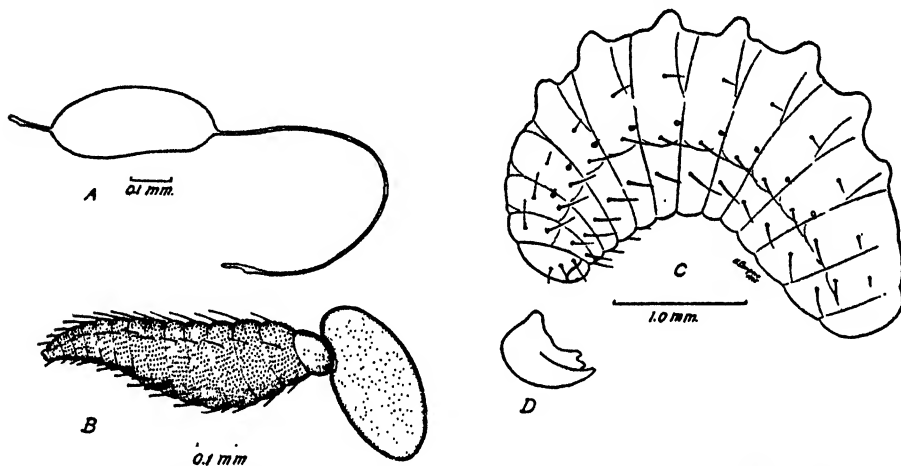
Fig. 2.—*Lecaniobius utilis* n. sp. *A*, egg; *B*, first-instar larva eating egg of black scale; *C*, full-grown larva; *D*, mandible of full-grown larva.

Lecaniobius utilis is established in California in at least one orchard in Ventura County.

Biology.—According to S. E. Flanders, *Lecaniobius utilis* reproduces readily under insectary conditions. At temperatures between 75° and 80° F. the life cycle from egg to adult is about thirty-eight days. The males usually appear several days before the females. The ratio of males to females is about one to two.

The female begins to oviposit the day after its emergence from its host. Its eggs are placed beneath mature scales. Scales that have just commenced to oviposit or are about to begin are the preferred hosts. The parasite first inspects the host from all sides. If satisfied with the preliminary inspection, it faces away from the scale and thrusts the ovipositor backward underneath the scale. If, after exploring the cavity beneath the scale with the ovipositor the parasite finds the scale suitable, an egg is deposited. The egg, shown in figure 2, adheres to the venter of the scale or to the host plant beneath by the adhesive tip of the long posterior stalk. Several eggs may be deposited beneath one scale. All the eggs may hatch, but as a rule only one larva completes its development. The parasite egg hatches in about two days. If no host eggs are available for the newly hatched larva to feed upon, it may remain quiescent for two weeks or more. During this period the larva appears to decrease some-

what in size. Several larvae were found in the act of entering the vagina of the scale.

The larvae are white and somewhat similar in size and shape to the larvae of *Scutellista*. They may be readily distinguished from the latter, however, by the presence of stiff, yellowish brown hairs sparsely scattered over the body, as shown in figure 2. In the laboratory the larval period lasted fourteen days.

In the orchards *Lecaniobius utilis* appears to overwinter as mature larvae. On June 13, 1935, one hundred mated females of *Lecaniobius* were liberated near Oxnard, California. The progeny of these were observed ovipositing in the following October. In December, however, no adults were observed in the field, although full-grown larvae were underneath the scales.

In the laboratory, pupation occurs three days after the larva has voided its meconium. At first the pupa is dull white, but within twelve hours it turns to dull black. The length of the pupal stage varied from sixteen to twenty-one days; the males have the shorter period. The complete life cycle from egg to adult is approximately thirty-eight days.

3. *Coccophagus heteropneusticus* n. sp.
(Fig. 3)

A medium-sized, black to dark brown species with the front and middle tibiae generally wholly white. In my key[4] to the species of the genus *Coccophagus,* this species runs to *C. yoshidae* Nakayama. It differs from the latter in the shape of the body by different chaetotaxy and wing characters. In this species the submarginal vein is longer than the marginal vein, and the group of three or so coarse setae on the outer margin at the base of the middle tibiae is lacking.

Female.—Dominantly black, often fading to dark brown on the sides and beneath. The following parts more or less orange-yellow; antennae, face in proximity to the antennal sockets, pattern on dorsum of the head, tegulae, parapsides except for a black spot anteriorly on the expanded part, sclerites near insertion of forewings, extreme apex of abdomen. Legs black or dark brown marked with white as follows: front and middle tibiae usually wholly, hind tibiae toward the apex and less extensively toward the base, apical ends, and a narrow annulus at the base of front and middle femora, tarsi except those of front legs and the apical one or two joints of the other legs, which are generally dusky.

Scape about five times as long as wide and as long as the pedicel and first funicle joint combined. Pedicel about two-thirds as wide as long and plainly shorter than the first funicle joint. First funicle joint the longest, slightly less than twice as long as wide. Second and third funicle joints decreasing in length so that the third is about as wide as long. Club short, not much wider than the funicle, the three club joints combined about as long as the two preceding funicle joints.

Shape of body, chaetotaxy, and wings as shown in figure 3.

The size is variable. The largest specimens which developed singly in immature *Saissetia oleae* (Bern.) measured 1.4 mm.

Male.—The males closely resemble the females and can be easily associated by the similarity.

Described from 72 specimens, holotype, allotype, and paratypes, as follows: 13 females ex *Saissetia oleae* (Bern.), Buenos Aires, Argentina, February, 1935; 15 females ex either *S. hemisphaerica* (Targ.) or *Coccus hesperidum* Linn., Buenos Aires, February, 1935; 2

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[4] H. Compere, A revision of the species of *Coccophagus*, a genus of hymenopterous coccid-inhabiting parasites, Proc. U.S. Nat. Mus., 78(7):11, 1931.

females ex *Saissetia oleae*, Campinas, Brazil, November, 1934; 1 male ex *Coccus viridis* Green., Campinas, November, 1934; 2 females ex *Saissetia hemisphaerica*, São Salvador, Brazil, October, 1934; 1 female ex *S. oleae*, São Salvador, October, 1934; 1 female ex *S. oleae*, Nictheroy, Brazil, December, 1934; 7 females and 1 male ex *S. oleae*, Rio de Janeiro, Brazil, December, 1934; 7 females and 1 male propagated on *S. oleae* in the quar-
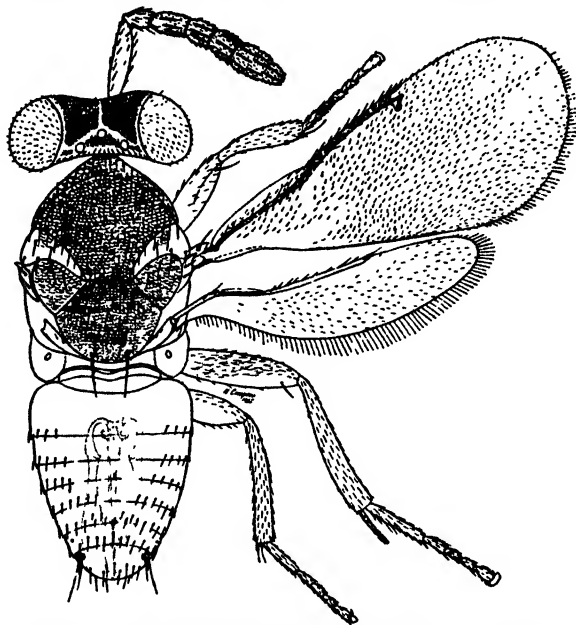
Fig. 3.—*Coccophagus heteropneusticus* n. sp. Female.

antine room at Riverside, September, 1935; 3 males ex *Pseudococcus citri* (Risso), Buenos Aires, February, 1935; 14 males ex *P. citri* in the quarantine room at Riverside, August, 1935; 1 female and 3 males reared at Riverside from Brazilian material.

The insectary records show that 625 *Coccophagus heteropneusticus* n. sp. were reared at the insectary from South American material. Of this number 426 were males obtained from a shipment of *Pseudococcus citri* (Risso) collected in Buenos Aires. The biology of this species has been published by S. E. Flanders.

4. *Coccophagus fallax* n. sp.

(Fig. 4)

A medium-sized species, thorax and abdomen black except for the posterior two-thirds or so of the scutellum, which is bright lemon-yellow. Legs yellow except the middle and hind coxae and most of the hind tibiae, which are black. Scutellum with from four to fourteen setae in addition to paired bristles, the apical pair of bristles long and coarse, the median and anterior paired bristles in most specimens not much longer than the scattered setae situated between them mostly on the anterior blackened part. Although this species runs to the *scutellaris* group in my key[5] because of the setose scutellum, it is not so closely related to them as it is to the *lycimnia* (*lecanii*) group of species.

[5] H. Compere, A revision of the species of *Coccophagus*, a genus of hymenopterous coccid-inhabiting parasites, Proc. U. S. Nat. Mus., 78(7):11, 1931.

Female.—Thorax and abdomen black except for the posterior two-thirds or so of the scutellum, which is bright lemon-yellow. Head partly orange-yellow to pallid yellow with more or less brownish or fuscous suffusions, the space within the ocellar triangle blackish. Antennae orange-yellow, legs yellowish white except for the greater part of the hind tibiae and the middle and hind coxae, which are black.

Scape four times as long as wide and a trifle narrower than the pedicel. Pedicel almost one and one-half times as long as wide and slightly but plainly shorter than the first funicle joint. First funcle joint slightly the longest; second and third subequal, about as wide as long. Club almost as long and as wide as the funicle. Funicle and club with numerous sensoria extending the length of the segments, as shown in figure 4.
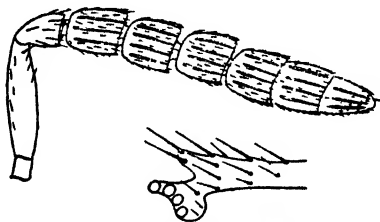
Fig. 4.—*Coccophagus fallax* n. sp.
Female, antenna and apical venation.

Forewings hyaline, twice as long as wide. Marginal vein a trifle longer than the submarginal vein (11:10); stigmal vein as shown in the figure. Wings ciliated as in the *lycimnia* group of species; the posterior basal hairless streak slightly upturned at the distal end and interrupted by three or four cilia from a weakly defined hairless spot.

Scutellum one and one-third times as wide as long and about as long as the mesoscutum.

Scutellum with a pair of strong apical bristles and a weak anterior and median pair often not much stronger than the scattered setae. A single female from Bahia has in addition to three well-developed pairs of bristles four smaller bristles or setae centered between the anterior and median pairs of bristles. The specimens from Rio de Janeiro have from ten to fourteen setae not much weaker than the anterior and posterior bristles.

Length, 1.1 mm.

Male.—Scutellum entirely black. Face and lower portion of head bright lemon-yellow. Parapsides more or less suffused with orange. Dorsum of the head, except within the space bounded by the ocelli, orange-yellow. Legs colored as in the females.

Length, 0.9 mm.

Described from 9 females and 1 male, holotype, allotype, and paratypes, reared from *Saissetia oleae* (Bern.) as follows: 5 females on one slide, Nictheroy, Brazil, September, 1934; 1 female reared at Riverside from black scale on *Cassia splendens* received from São Salvador, Bahia, Brazil, October, 1934; 3 females on tags in a miscellaneous lot of Brazilian parasites without date or locality data; 1 male on slide from São Salvador, Bahia, Brazil.

Coccophagus fallax was at first incorrectly identified, and no attempt was made to propagate it for colonization. It was first thought to be *C. lycimnia* Walker, a species occurring in California.

5. *Coccophagus lycimnia* Walker

Aphelinus lycimnia Walker, Mon. Chalc., 1:12, 1839.
Coccophagus lycimnia Mercet, Eos, 7(4):400, 1931.

Three slide-mounted specimens reared from *Saissetia oleae* (Bern.), on *Cassia imperialis*, at Nictheroy, Brazil, on September 5, 1934, are questionably referred to this species. To these three specimens is ascribable in part the failure to recognize *Coccophagus fallax* as a new species when the collec-

tions were made. *C. lycimnia* and *C. fallax* are similar in size and resemble each other in coloration and are hardly distinguishable unless the specimens are mounted and examined with a lens.

Coccophagus lycimnia Walker is presumably the same as the species already occurring in California, where it has been known under the name *Coccophagus lecanii* (Fitch).

6. *Coccophagus basalis* n. sp.
(Fig. 5)

This small-sized species can be determined by its distinctive coloration in combination with the following diagnostic characters: scutellum with three pairs of setae; pedicel slightly longer than the first funicle joint; ovipositor concealed.

Female.—Dominantly black with a broad yellow band across the base of the abdomen. On the dorsum of the abdomen the yellow band occupies the first tergite, ventrally it expands so that the greater part of the underside is yellow. Head dominantly dark brown or blackish except the temples and posterior lateral corners of the frontovertex, which are orange. Antennae yellow; legs dominantly white with variable fuscous markings as follows: basal half or so of front femora; middle femora except the ends; front coxae. Middle and hind coxae white or mostly so, occasionally fuscous toward the base. Front tibiae faintly dusky. Scape slightly more than four times as long as wide, as wide as the pedicel. Pedicel

Fig. 5.—*Coccophagus basalis* n. sp. Female,
antenna and apical venation.

one and one-half times as long as wide and one and one-half times as long as the first funicle joint. First funicle joint a trifle smaller than the following and slightly longer than wide. Second and third funicle joints equal, each a trifle longer than wide (5:4). The club as long as the funicle, the three joints subequal, each about as long as the third funicle joint and the first two a trifle wider than the funicle as shown in figure 5.

Mandibles with two small teeth and a broad truncation.

Forewings almost imperceptibly smoky, three times as long as wide; cilia moderately dense and not forming a bare spot or speculum beneath the submarginal vein. Submarginal vein slightly shorter than the marginal vein (4:5); stigmal vein as shown in the figure.

Scutellum wider than long (6:5) and shorter than the mesoscutum (5:7). Abdomen about as wide and as long as the thorax. Ovipositor very short, hardly more than one-third as long as the abdomen, not exserted.

Dorsum of head with short, coarse, black setae. Eyes plainly hairy. Mesoscutum rather densely setose, the setae coarse, six or so longer and coarser setae along the posterior margin and along the parapsidal margins. Parapsides with four setae on each and axillae with three setae on each. Scutellum with three pairs of stout bristles. Strong, coarse setae on all tergites except the first. Apices of front femora with a coarse, black seta beneath, plainly larger than the seta similarly placed on the middle femora. Tibial spur of middle legs slightly shorter than the basitarsus, the basitarsus as long as the succeeding three segments united.

Length, 1.0 mm.

Male not known.

Described from 36 females, holotype and paratypes, obtained as follows: 1 captured on cassia leaf infested with *Saissetia oleae* (Bern.), Nilopolis, Federal District, Brazil, August

29, 1934; 4 from *S. oleae*, Nictheroy, State of Rio de Janeiro, August and September, 1934; 4 from *S. Oleae*, Rio de Janeiro, September, 1934; 3 from *S. hemisphaerica* (Targ.) on olive tree, São Salvador, Bahia, October, 1934; 2 from *S. oleae* at Riverside from material imported from São Salvador, Bahia, October, 1934; 20 females from *S. hemisphaerica*, Nictheroy, January, 1935.

This species develops in the small-sized scales and is supposedly a primary parasite. The attempts to propagate it in the insectary at Riverside were unsuccessful. The insectary records show that 128 live specimens were reared at Riverside from *Saissetia oleae* (Bern.), imported from Brazil. Only females were obtained. These oviposited readily in first- and second-instar black scale, but no adult progeny were secured. Dissections revealed unhatched eggs containing perfectly formed larvae.

7. *Aneristus brasiliensis* Compere
(Fig. 6)

This species was described[e] from two females reared from *Saissetia oleae* (Bern.) by E. J. Hambleton at Viscosa, Minas Geraes, Brazil, in May and
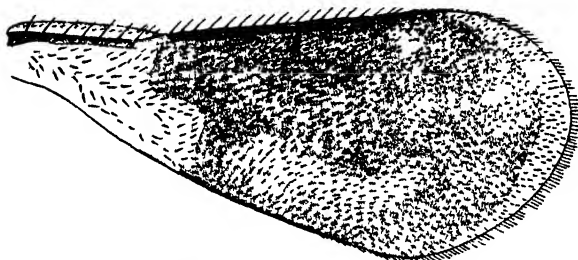
Fig. 6.—*Aneristus brasiliensis* Compere. Female, forewing.

August, 1933. *Aneristus brasiliensis* is one of the commonest parasites of black scale in Brazil. It was particularly abundant in material collected at Rio de Janeiro and Nictheroy. "Rubber sized" black scales are the preferred hosts. The failure of this species to reproduce in the insectary at Riverside is unexplained. The records show that at least 146 adults were reared and counted. These were given an opportunity to reproduce on black scale in cages in the quarantine room.

8. *Aneristus oculatipennis* Girault

Aneristus oculatipennis Girault, Psyche, 23:42, 1916. Dozier, Jour. Dept. Agr., Porto Rico, 16(2):97, April, 1932.

Three females of this species were reared from *Saissetia oleae* (Bern.) infesting *Cassia splendens* collected at São Salvador, Bahia, Brazil, October 6, 1934; according to the Citrus Experiment Station records, Flanders reared 3 females at Riverside from material imported from Bahia, Brazil.

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[e] H. Compere, Notes on the classification of the Aphelinidae, Univ. Calif. Publ. Entom., 6(12):287, 1936.

9. *Aneristus pallidiceps* n. sp.
(Fig. 7)

This species can be distinguished by the infuscated pattern of the fore-wings and by coloration.

Female.—Dominantly black except the frontal aspect of the head, which varies from pale straw color or dirty white to brownish with fuscous suffusions. Scape concolorous with the face, remainder of antennae blackish. Legs mostly black marked with white as follows: all tarsi except distal ends; front tibiae and knees of front and middle legs; tibial spur of middle legs.
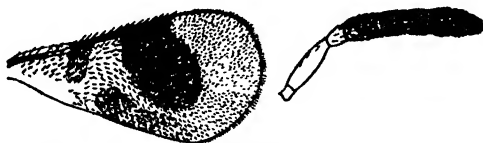
Fig. 7.—*Aneristus pallidiceps* n. sp. Female,
forewing and antenna.

Forewings and antennae as shown in figure 7.

Described from 4 females, holotype and paratypes. These specimens were reared in the quarantine room at Riverside by S. E. Flanders from *Saissetia oleae* (Bern.). The black scale was on twigs of *Cassia splendens* collected at São Salvador, Bahia, Brazil, October 6, 1934, by H. Compere.

The insectary records show that 8 live females were obtained at Riverside from black scale imported from Bahia, Brazil. According to Flanders, this was the only species of *Aneristus* to reproduce in the insectary. Only a few specimens of a second generation were obtained, and the stock died out. The females drilled the dorsum of the scale, explored the inside with the ovipositor, and then laid an egg in the gastric caecum. The life cycle at approximately 80° F. was less than forty days. One female of a second generation was obtained.

10. *Tomocera* sp.?

Two female pteromalids which in many characters resemble the genus *Tomocera* Howard were reared from *Saissetia oleae* (Bern.) collected near Campinas, Brazil, in November, 1934.

11. *Euaphycus* sp.

A species of *Euaphycus* was found parasitizing the younger stages of black scale on *Hedera helix* in the back yard of a residence on Avenida Paulista, São Paulo, Brazil. Few live scales containing parasites were present. The number of dead scales with exit holes showed that previously the *Euaphycus* had been plentiful. The insectary records show that Flanders obtained 4 specimens of *Euaphycus* from a shipment of this material.

12. *Encyrtus* sp.

A single specimen of a species of *Encyrtus* was reared at Rio de Janeiro from *Saissetia* on cassia collected in Nictheroy. The cassia was heavily infested with *S. oleae*. It is now suspected that a few stray *S. hemisphaerica* (Targ.) were mixed with the *S. oleae* and that probably the *Encyrtus* sp.

issued from *S. hemisphaerica.* Apparently what is the same species of *Encyr-tus* was reared from *S. hemisphaerica* collected at Bahia, Brazil. In Nictheroy, where the *S. oleae* was injurious on cassia trees, near-by *Ficus benjamani* were heavily infested with *Saissetia hemisphaerica.*

13. *Gahaniella saissetiae* Timberlake

Gahaniella saissetiae Timberlake, Proc. U. S. Nat. Mus., 69:27–28, 1926.

A species of *Gahaniella,* apparently the same as *saissetiae* Timberlake, was reared in large numbers from black scale collected in Brazil. All the evidence indicates that this is an injurious hyperparasite. A suspicion that the species was not a primary parasite arose when the oviposition habits were observed. *Gahaniella* thoroughly explored uninhabited scales with the ovipositor but did not deposit eggs. After the first few shipments, all *Gahaniella* were destroyed in the quarantine room.

14. *Eupelmus coccidivorus* Gahan

Eupelmus coccidivorus Gahan, Proc. U. S. Nat. Mus., 65(4): 6, 1924.

This species, which failed to reproduce in the quarantine room at Riverside, is suspected to be an injurious hyperparasite. A total of 248 specimens were reared in the quarantine room at Riverside from *Saissetia oleae* (Bern.) imported from Brazil. *Eupelmus coccidivorus* is one of the species commonly obtained from black scale in Brazil. This determination has been corroborated by A. B. Gahan.

15. *Eupelmus* sp. ?

Fourteen specimens of an undetermined eupelmid were reared in the quarantine room at Riverside from *Saissetia oleae* (Bern.) imported from Brazil.

16. *Eurytoma* sp. ?

Forty-eight specimens of an undetermined eurytomid were reared in the quarantine room at Riverside from *Saissetia oleae* (Bern.) imported from Brazil. Nothing is known regarding its habits.

17. *Diplosis* sp. ?

Seventy specimens of a *Diplosis,* or a closely related genus, were reared in the quarantine room at Riverside from *Saissetia oleae* (Bern.) imported from Brazil. This is a primary species. It was collected at Rio de Janeiro in one locality in the city. Numerous puparia were noticed under some of the black scale.

18. *Azya orbigera* Mulsant
(Figs. 8, 9)

Two species of *Azya* were occasionally found feeding upon *Saissetia oleae* (Bern.) in Brazil. In no place were the beetles or larvae abundant. Twenty-six *Azya* spp. were obtained at Riverside from material imported from Brazil. One of the species, *Azya orbigera* Muls., reproduced at Riverside. A breeding

stock has been maintained and colonies liberated. In the fall of 1935, *Azya* larvae were observed on trees infested with black scale in one orchard in Ventura County, where a colonization had been made.

Azya orbigera, as shown in figure 8, is a hemispherical coccinellid, 3 to 4 mm. in diameter. The dorsum is black, covered with a fine, white pubescence

Fig. 8.
*Azya
orbigera*
Mulsant.
Female.

except for a large circular bare spot on each elytron. The abdomen is reddish brown. The males are easily separated from the females by the yellow face and emarginate sixth abdominal segment. Both sexes occur in about equal numbers.

Biology.[7]—Mating takes place about one to two weeks after the adults emerge. This fact should be taken into consideration when making liberations. Oviposition occurs soon after mating. The female may be observed standing on a mature black scale with the ovipositor curved downward and under the body of the host beneath it. The egg is large, smooth, yellow, and somewhat elongate.

The incubation period is a little over six days. Newly hatched larvae are bright yellow with black ocelli. They soon begin to secrete thick, waxy filaments, as shown in figure 9. During the early instars the longest filaments are on the center of the dorsum. In the later stages the lateral and caudal filaments about equal the length of the median dorsal row of filaments. The larval period requires about fifteen days. Mature larvae crawl to the ground and pupate in protected places. The pupae are orange-yellow, covered with brownish hairs, and entirely hidden from view by a covering of wax. The pupal period is about nine days at 80° F.

The entire life cycle is completed in approximately thirty days. This species appears to feed only on the eggs and immature stages of the black scale; the very young feed on the eggs and first-instar scale, and the more mature larvae and adults feed on the larger scales. The coccinellids obtain the food, which consists almost entirely of the body fluids of the host,

Fig. 9.—*Azya orbigera* Mulsant. Partly grown larva.

piercing the dorsum of the host with their mandibles. Since the integument of the scale is left behind, there is often an apparent abundance of food when in fact there is none. A single larva is able to destroy large numbers of scale. This coccinellid reproduces readily in the insectary. If food enough is available, more than 100 progeny may be reared from a single female.

On August 13, 1935, 70 specimens were released at Oxnard, California. Two months later larvae were found on the trees upon which the adults were liberated. Since then, however, none have been observed, and the establishment of the species is doubtful.

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[7] Note on biology contributed by S. E. Flanders.

A REVISION OF THE STREPSIPTERA
WITH SPECIAL REFERENCE TO
THE SPECIES OF NORTH AMERICA

BY

RICHARD M. BOHART

CONTENTS

A REVISION OF THE STREPSIPTERA WITH SPECIAL REFERENCE TO THE SPECIES OF NORTH AMERICA

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INTRODUCTION

THE STREPSIPTERA form a group of peculiar insects numbering about three hundred described species from all parts of the world. Because of the many unusual features of their biology and their striking structural modifications, they have been a favorite subject for philosophical speculation by entomologists since the early part of the nineteenth century. Since they most frequently parasitize aculeate Hymenoptera or auchenorhynchous Homoptera, they are usually found as wormlike or pupiform parasites in these hosts. The mature females are characterized more by the absence of characters than by their presence. Thus, a typical example from a fulgorid lacks eyes, antennae, palpi, thoracic and abdominal segmentation, legs, wings, and genitalia. The male of the same species, however, is a highly organized insect with great, fanlike hind wings, and small forewings which resemble the halteres of Diptera. The anomalous appearance of the Strepsiptera has given rise to a great diversity of opinion concerning their systematic position. Furthermore, many genera and species have been based solely on the relatively characterless females.

The author has been fortunate in being able to study the largest collection of Strepsiptera types in the world at the United States National Museum and the extensive collections at the Harvard Museum of Comparative Zoölogy and the California Academy of Sciences. In addition, the author's private collection numbers well over a thousand specimens. These studies have resulted in much additional information on the biology and morphology of less well known forms. On this basis a revised classification is given which the author hopes will clarify much of the existing taxonomic confusion of the group.

ACKNOWLEDGMENTS

brother, Mr. G. E. Bohart, for the collection of a large amount of the material used in this study; and particularly to Mr. H. S. Barber for many helpful suggestions and valuable criticism.

HISTORY

The first record of a strepsipterous insect was made in 1793 by Petrus Rossius, who discovered the males parasitic in *Polistes gallicus* Linn. He gave them the name *Xenos vesparum,* a new genus and species, and, reasoning from the apparent similarity of habit, placed the genus in the Hymenoptera next to *Ichneumon.* Subsequently Rossius' species was placed by Latreille (1809) in the Diptera, tribe Phthiromyae. In 1802 William Kirby described the parasite of *Andrena nigroaena* Kirby as *Stylops melittae* but failed to associate it with Rossius' species until 1815 when he erected the new order Strepsiptera, basing the name on the twisted front wings usually found in pinned specimens. In the same paper Kirby named the first North American species, *peckii;* the specimen was sent to him by Professor Peck. Although Kirby considered these insects deserving of a special order of their own, he did not recognize the differences between larvae, pupae, and mature females and, in fact, believed the winged forms to be females and the male aedeagus to be the female ovipositer. Furthermore, the first larvae were unknown to him and on the advice of his delineator he considered the male elytra to be appendages of the front coxae.

At about the same time two additional names were given to this group. In 1816 Lamarck treated it as the dipterous family Rhipidoptera, and in 1817 Latreille created for it the order Rhipiptera.

During the next half century, the Strepsiptera were shifted from order to order and treated in various degrees of rank from a subfamily to a distinct order. As an example of the taxonomic misconceptions with respect to them during these years, Swainson in the "History and Natural Arrangement of Insects" (1840) placed them as the family Stylopidae in the old order Neuroptera between the Forficulidae and Phyrganidae (Odonata and Ephemerida). Also, he referred to the first larvae as parasites emerging from the *Stylops* larvae in bees and provisionally assigned them to *Pediculus.*

However, toward the end of the nineteenth century the majority of entomologists considered the Strepsiptera to be either Coleoptera or a distinct order.

The principal works on embryology and anatomy are those of Nassonow (1892, 1893), who published several papers in Russian, Brues (1904), and Smith and Hamm (1914). One excellent paper on systematics by Perkins appeared in 1905.

The most important contribution in recent years was that of W. D. Pierce who in several papers (1908–1918) brought together most of the information on the group and described and figured many new forms. Since 1918 the workers have been almost entirely European, Hofeneder, Ulrich, and A. Ogloblin contributing several critical papers.

SYSTEMATIC RELATIONSHIPS

The arguments for separation of the Strepsiptera as a distinct order unrelated to Coleoptera have been most fully presented by Pierce (1909, 1918). Since that time, however, new discoveries have been made which have thrown additional light upon the subject. In 1919 Peyerimhoff described the female and first larva of *Eoxenos laboulbenei*. Subsequent researches by Parker and Smith (1933, 1934) and Silvestri (1933) have shown that this species is typical of the mengeid type of Strepsiptera formerly known only from the male. The female emerges from its puparium as an adult and represents the only mature female Strepsipteran which can readily be called coleopterous in appearance.

In a recent paper Pierce (1936) has reaffirmed his stand. He considers the Strepsiptera an order related to "Psylloptera," "Aleurodoptera," "Coccoptera," and Diptera, all of which are treated as orders. The last two, together with the Strepsiptera, are classed as "Dipteroid, pupariate." In support of this contention he cites, as characters common to this "dipteroid" group, the tendency to transform within a puparium, the occurrence of wingless females, ovoviviparity, and the presence of two wings and two "balancers." However, these characters do not necessarily eliminate the Strepsiptera from the Coleopteroidea. Certain beetles, notably in the meloid subfamily Nemocognathinae, pupate within a puparium, wingless females occur in many orders including Coleoptera, and ovoviviparity occurs in the micromalthid beetles. Finally, Pierce's comparison of "balancers" and "wings" irrespective of the segments on which they occur appears illogical. On the contrary, it would seem that the matter of wings constitutes one of the strongest arguments for allying the Strepsiptera with the Coleoptera, which alone among the large holometabolous orders depends largely on the hind wings in flight.

Unfortunately, the links which would connect the Strepsiptera with more ordinary beetles are almost entirely unknown. As a result, the relationship of the group must be largely based on a comparison with coleopterous families which have pursued a parallel evolutionary course, that is, toward endoparasitism.

The principal coleopterous families containing forms whose biology is comparable with that of the Strepsiptera are Carabidae, Staphylinidae, Micromalthidae, Meloidae, and Rhipiphoridae. Of these the last two, because of their more strictly parasitic tendencies, lend themselves most readily to purposes of comparison. In general the Rhipiphoridae are more specialized than the Meloidae and present a nice picture of phylogeny, beginning with the mordelloid genera *Pelecotoma, Trigonodera,* and *Toposcopus,* followed by the more modified *Macrosiagon* and *Rhipiphorus,* and ending with the highly specialized *Rhipidius* and *Rhyzostylops,* which approximate the primitive Strepsiptera. It should be stated at this point that in the present paper no attempt is made to ally the Strepsiptera closely with the Rhipiphoridae. The totally different structure of the hind wings and metathorax and the non-heteromerous tarsi of the former argue strongly against such a course. For

convenience it may be assumed that, with respect to any given similarity, each group has reached the same stage in progressive modification and that, therefore, a close relationship is not necessarily implied. As indicated by the fossil record, the Strepsiptera and Heteromera were undoubtedly separated long before Tertiary times, but subsequent to that separation each has followed a similar line of evolution, namely, toward endoparasitism. However, the Strepsiptera have developed in their more modified forms a state of endoparasitism almost without rival among the parasites of insects. In the Rhipiphoridae only the most modified genera, notably the cockroach parasite, *Rhipidius,* even partially approach this condition.

Notwithstanding this fact, the similarities between the Rhipiphoridae and Strepsiptera are nonetheless striking. In the adult male the raspberrylike eyes with large, well-separated facets and the narrow, hairy, soft-textured elytra, typical of the Strepsiptera, are found in *Rhipidius.* Pectinate antennae are common to both groups, and the more specialized rhipiphorids have radial wing venation.

The free-living adult female Strepsipteron has the head distinct and provided with four- to five-segmented simple antennae, two-segmented maxillary palpi, reduced mandibles of a distinctly biting type, and eyes which are aggregations of large facets. The thorax is divided into the usual three segments, of which the prothorax is the largest, each segment bearing a pair of legs with three- to four-segmented tarsi and claws. This female can be compared favorably with larviform females found in various families of Coleoptera but is most nearly paralleled by the rhipiphorid, described by Silvestri (1905) as *Rhyzostylops inquirendus.*

The first larva or triungulin of the Strepsiptera is without well-formed antennae or mandibles, the maxillae are reduced, and all the legs are without trochanters. Otherwise there is little to distinguish them from various first larvae of hypermetamorphic Coleoptera. The eyes are composed of large, well-separated facets located in a pigmented area. They are of the same type as that found in *Rhipiphorus* and *Rhizostylops.* The mouthparts of meloid and rhipiphorid first larvae show a reductional transition exemplified by *Meloe* to *Tetraonyx* to *Rhipiphorus* and *Rhizostylops.* The maxilla of the triungulin larva of the strepsipteron, *Stichotrema,* is remarkably similar to that of *Rhizostylops.*

To summarize, it can be said that the Strepsiptera and Rhipiphoridae possess among some species similar endoparasitic habit, hypermetamorphosis, campodeiform first-stage larvae, sexual dissimilarity of adults, wingless adult females, berrylike eyes with distinct facets in both sexes, ramose male and simple female antennae, radial wing venation of the hind wings in the male, strongly reduced male elytra, reduction of the prothorax, enlargement of the metathorax, and diminution of the abdomen in the male.

It is difficult to consider this remarkable parallelism as existing between two unrelated groups of insects although it is true that many of these characters are not in themselves of fundamental phylogenetic importance.

Finally, from the standpoint of fundamental ordinal characters, the Strepsiptera are holometabolous, have legged first larvae, exarate pupae, adult mouthparts of an essentially biting type, free prothorax, reduced mesothorax and mesothoracic wings, and enlarged metathorax, the wings of which are largely depended upon in flight. The foregoing statements apply equally well to the less specialized Coleoptera.

However, several striking dissimilarities are evident. Unlike Coleoptera, Strepsiptera have no differentiated trochanters. Furthermore, the tremendously enlarged vannal area of the hind wings, the accompanying development of the metathorax, and the diminutive prothorax are not found in any Coleoptera. In addition to these differences, the obvious objection to following customary practice and including them in the Heteromera is that the Strepsiptera are isomerous.

For these reasons the group is treated here as an order closely allied to the Coleoptera. The author's conception of the phylogenetic relationships is graphically illustrated in figure A, 11.

EXTERNAL MORPHOLOGY AND PHYLOGENY

Within the order Strepsiptera the prevailing trend has been toward specialization by reduction. This tendency is very evident in the external morphology of both the adults and the first larvae.

Progressive reduction is most completely demonstrated by the adult male. The antennae are flabellate and thickly covered with relatively large sensoria. The segments vary in number from seven to four, and at least the third has a lateral flabellum. The antennae are six- to seven-segmented in the Mengeidae (fig. B, 1–4), seven-segmented in Halictophagidae (fig. H, 1–5) and Myrmecolacidae (fig. C, 8), six- to four-segmented in Stylopidae (fig. F, 2, 4), five-segmented in Callipharixenidae, and four-segmented in Elenchidae. Except in Elenchidae and a few species in which it may be absent, all male Strepsiptera have a large round sensorium near the base of the fourth antennal segment. In elenchids, where an obvious fusion has taken place between the third and fourth segments, this sensorium is found on the third (fig. H, 6).

The eyes of male Strepsiptera are characterized by their large, well-separated facets giving the appearance of a raspberry. It has been asserted that they are not homologous with the eyes of adult Coleoptera but are actually aggregations of simple eyes. The work of Strohm (1910) indicates that each facet corresponds to a lateral ocellus. A similar assertion has been made with respect to the adult male Coccidae, whose eyes bear a strong superficial resemblance to those of Strepsiptera. Although such a phenomenon is unknown in adult beetles, the structure of the eyes of *Rhipidius* and of larviform female Lampyridae may possibly be of this type. Also, if the assumption is allowed that the seemingly reduced compound eyes of male Strepsiptera are indeed clusters of lateral ocelli, it is not certain that they could not have developed from the genetically related compound eyes, which are similarly innervated by the optic lobes of the brain.

In the primitive family Mengeidae, *Mengea* and some species of *Mengenilla* possess both labium and labrum in a reduced form, whereas all other genera of Strepsiptera are lacking in this respect. The mandibles are similar throughout the group, being broad and scimitar-shaped except in *Triozocera* and the genera derivable from it, *Myrmecolax* and *Caenocholax*. In these three genera the mandibles are reduced and almost bristlelike. The maxillary palpi are two-segmented in all genera. Maxillae proper and labial palpi are absent.

The prothorax and mesothorax are strongly reduced in all known Strepsiptera. The metathorax, however, is powerfully developed.

In the metathorax the prescutum is weakly differentiated in the Mengeidae but distinct in the other families (fig. A, 5, 6, Prs.). Its relative size is apparently related to the shape of the hind wings. Thus, in the Halictophagidae and Elenchidae, the prescutum is usually longer than the scutellum, and the wings are correspondingly narrowed (fig. H, 32). In the few species of Halictophagidae with a small prescutum, the wings are broader. A similar condition exists in the Myrmecolacidae, in which the prescutum is very large and the wings are relatively narrow. Conversely, in the Stylopidae and Callipharixenidae the prescutum is small and the wings are broad (fig. C, 1).

The postlumbium represents the enlargement of the interclerital membrane between the scutellum and postscutellum. It varies greatly in shape, ranging from a narrow transverse band to a broad, roughly semicircular area (fig. A, 8, 9, Plb.).

The postscutellum is the most prominent part of the metathorax and is more strongly developed than in any Coleoptera. In most beetles it is an insignificant sclerite and is conspicuous only in a relatively few, such as the Phengodidae (fig. A, 7, PScl.). In Strepsiptera it varies from the small sclerite in *Mengenilla* (fig. A, 5, PScl.) to the greatly modified condition in *Stylops* and other modified genera. Since the third axillary sclerite of the hind wing is connected through a peculiar, club-shaped, intermediate piece with the base

FIG. A

1. *Eoxenos laboulbenei* Peyerimhoff, hind wing (Mengeidae).
2. *Priacma serrata* Lec., hind wing (Cupesidae).
3. *Blatella germanica* Linn., articulation and basal venation of the hind wing (Blattidae).
4. *Pterotus obscuripennis* Lec., articulation and basal venation of the hind wing (Phengodidae).
5. *Xenos pallidus* Brues, articulation and basal venation of the hind wing (Stylopidae).
6. *B. germanica*, metanotum.
7. *P. obscuripennis*, metanotum.
8. *Mengenilla santcchii* (Pierce), metanotum (Mengeidae).
9. *Triozocera mexicana* Pierce, metanotum (Mengeidae).
10. Strepsiptera, schematic phylogeny and host relationships.
11. Coleoptera, schematic phylogeny.

C. Costa.
Cu. Cubitus.
J. Jugal vein.
M. Media.
PCu. Postcubitus.
Plb. Postlumbium.
Prs. Prescutum.

PScl. Postscutellum.
R. Radius.
Sc. (figs. 1–5) Subcosta.
Sc. (figs. 6–9) Scutum.
Scl. Scutellum.
V. Vannal vein.

Fig. A.

of the muscle-filled postscutellum, the latter undoubtedly plays an important part in the motivation of the vannal area of the wing. Thus it is possible to explain the observations of Parker and Smith (1934) and others that the males of *Eoxenos* and *Mengenilla,* which have the postscutellum weakly developed, do not maintain a continuous rapid vibration of the hind wings as do stylopids, halictophagids and elenchids.

Much of the unique appearance of male Strepsiptera is due to the wings. The forewings in all known species are small, paddle-shaped or clublike structures, which have entirely lost the protective function of elytra. Their resemblance to the halteres of Diptera has been pointed out by many authors, and it appears likely that they may be analogous structures. Since the forewings are kept in constant motion and create a noticeable buzzing, it has been asserted that they serve to maintain muscle tone and equilibrium. Their anatomy has been carefully worked out by Ulrich (1930a).

The hind wings are remarkable for their reduced venation and great size. The author has attempted to homologize the veins with those of Coleoptera by studying the basal venation and axillary sclerites (fig. A, 1–5). The designation of the veins in the anal area of the wing as postcubital, vannal, and jugal follows Snodgrass (1935) in terminology. The illustration of *Eoxenos* (fig. A, 1) represents the most complex strepsipterous wing with the exception of that of the fossil, *Mengea,* which is imperfectly known. In *Eoxenos* the costa and subcosta are fused along the anterior margin of the wing. The articulation of the subcosta with the first axillary sclerite can be seen in the drawing of *Xenos* (fig. A, 5), which has almost identical basal venation. The radius of *Eoxenos* terminates before the wing margin and beyond it lie two detached pieces. It is fused at the base with the media, and the basal stem articulates with the second axillary sclerite. The media runs the entire length of the wing and is associated with two detached pieces distally. The cubitus, as in Coleoptera, nearly bisects the wing and also articulates with the second axillary sclerite. It consists in *Eoxenos* of two branches, the most anterior of which is detached at the base. Whether these two branches represent the cubitus and postcubitus of Coleoptera is a matter for conjecture. Only the more posterior vein is found in families other than the Mengeidae. Two vannal veins are present and a weak jugal, all of which articulate with the third axillary sclerite. In the fossil, *Mengea,* a cross vein occurs between the first vannal and second cubital veins. In the nomenclature of the medial and cubital veins of the cupesid wing figured, the author has followed Forbes (1924). However, this wing of *Priacma* is given as a generalized coleopteran type and not in order to show a similarity in appearance to that of *Eoxenos.* For comparison the primitive wing venation of the cockroach, *Blatella,* is represented in figure A, 3.

An attempt to homologize strepsipterous wings with those of Coleoptera is rendered particularly difficult because of the entirely different methods of folding the wing at rest. Most beetles have a more or less complicated system of oblique and transverse folding of the hind wing beneath the wing covers.

Although some rhipiphorids, buprestids, and others do not fold their wings transversely, this is apparently a recent deviation from the wing-folding type because most of its basic features are retained. They are of limited value for comparison with strepsipterous wings, in which the weak longitudinal folding is of much older origin.

A progressive reduction of the wing venation, closely paralleling that of the antennae, occurs in the Strepsiptera and finds its culmination in *Elenchus* on the one hand and *Crawfordia* on the other.

The legs are remarkable for their long front and middle coxae, absence of trochanters, and modified isomerous tarsi. Pierce (1918) claims to have distinguished a coxa and trochanter, the former existing as a minute basal segment in the front and middle legs; and this distinction has been followed by Ulrich (1927a). However, the author considers the trochanter distinguished by these investigators the true coxa, and the coxa which they note, a pleurite. G. F. Ferris of Stanford University, after an examination of material in the author's collection, agrees with this conclusion. The trochanter is presumably fused with the femur in all three pairs of legs. As in many Coleoptera, the hind coxae are much smaller than the front or middle pair.

The tarsi in the Mengeidae are five-segmented and terminated by two simple claws. All the segments are cylindrical except in *Triozocera*, in which the fourth is flattened and bilobed. In all the families in which copulation takes place with partially endoparasitic females, the tarsi are clawless, and the terminal segments are flattened and furnished with large pulvilli. In the Callipharixenidae, Myrmecolacidae, and Stylopidae the tarsi are four-segmented, the first named being the least specialized in this respect by virtue of its cylindrical basal segment. The Halictophagidae have three-segmented tarsi and those of the Elenchidae are only two-segmented. It can be seen, therefore, that reduction in number of tarsal segments nicely parallels the reduction in the antennae and wings.

The abdomen is ten-segmented and partially concealed beneath the post-scutellum. The latter differs widely in shape among the various genera. It can be said in general that in the Mengeidae, the females of which are free-living as adults, the aedeagus is nearly straight, whereas in all other Strepsiptera, with two exceptions, it is hooked at the end to enable the male to fertilize the partially endoparasitic female. The exceptions are the Elenchidae, in which the genital opening between the head and thorax of the female is very large, and the Callipharixenidae, in which fertilization takes place beneath the wing covers of the hemipterous hosts.

Female mengeids resemble the larviform adults of several coleopterous families. Their essential characteristics have been discussed in the section on systematic relationships. A more complete description is given by Parker and Smith (1933). All other female Strepsiptera are partially endoparasitic throughout adult life. Protruding from the host are the head and thorax, which are more or less fused to form a cephalothorax. The completeness with which they are fused is of some importance in phylogeny. Although immov-

able, the head can be distinguished in most genera, and in the Calliphari-xenidae and a few Stylopidae the three segments of the thorax are frequently discernible. In the stylopid genera *Hylecthrus* and *Halictoxenos,* however, the head is completely fused with the thorax (fig. B, 9, 10). It should be pointed out that the female referred to by most authors is actually the pu-parium or last larval skin within which the female is permanently sealed. Nevertheless, this is only a matter of interpretation because the puparium, through the role it plays in respiration, reproduction, and food absorption, is an integral part of the parasite.

In the Callipharixenidae and most of the Stylopidae the head is relatively small. In the Halictophagidae it is the dominant part of the cephalothorax, and in the Elenchidae it greatly overshadows the reduced thorax. The only distinguishing features of the head are the mouth opening and a reduced pair of mandibles. A single pair of metathoracic spiracles occurs in all endopara-sitic females. The large trachea from each enters and penetrates a short dis-tance within the respiratory tube of the true female. Pierce claims that he has found mesothoracic spiracles in *Callipharixenos.* After an examination of the type material of this genus at the United States National Museum, the author is inclined to agree with this assumption. Unfortunately, the spiracles cannot be seen clearly in the type-slide mounts.

The cephalothorax possesses one characteristic structure which is without parallel in the Insecta. The brood passage is the ventral space between the female and its puparium. It has a typically slitlike opening between the head and thorax of the puparium, at which point the true female is reinforced with ridges. It is through this opening that insemination takes place and the first larvae emerge. Copulation and emergence of first larvae in free-living mengeid females, however, is by means of a single posterior duct.

At the juncture of the cephalothorax and abdomen the integument of the puparium is often thickened and dark colored. The shape and color of this band is frequently of generic and specific significance.

The abdomen ends blindly without genitalia, but an anus is usually visible. The genital passages of the female are secondary in nature and occur on the second to fifth segments of the abdomen of the true female. They are single, median, tubelike invaginations with an open inner end. They represent sec-ondary oviducts and, as far as is known, occur in no other insects. They, as well as the brood passage, are lined with outward-pointing spicules to facilitate the emergence of the triungulins. In Stylopidae the number of genital tubes varies from two to five, the exact number constituting a generic character. In the Callipharixenidae five have been recorded for *Callipharixenos* and four for *Corioxenos.* Three or fewer are found throughout the Halictophagidae and Elenchidae. According to Hofeneder (1910*a*) the female genital pores of *Stichotrema* are arranged in three transverse rows of twelve to fourteen each. His observation has not been checked by later investigators, and it is difficult to homologize this situation with that found in other Strepsiptera.

The first larvae of the Strepsiptera have been called both triungulins and

triungulinids. The inappropriateness of the term triungulin as applied to the larvae of hypermetamorphic Coleoptera has been pointed out by other authors, and its application is justified only by common usage. Strepsipterous first larvae resemble those of Rhipiphoridae and Meloidae. They are minute, bristly hexapods with one or two pairs of posterior stylets. It is unfortunate that they are not known for every genus because their characters are very useful in classification. The form of the tarsi is particularly valuable from a phylogenetic standpoint. The simplest and perhaps the most primitive type is found throughout the Halictophagidae and Elenchidae. Here the tarsi are all bristlelike and without evident pulvilli. In the Mengeidae the front and middle tarsi bear small round pulvilli. The pulvilli of the Stylopidae, however, are very large; they are round in the parasites of wasps but elongate in the parasites of bees. An intermediate shape is found in the callipharixenid, *Corioxenos,* whose pulvilli are large and oblong.

Pierce (1918) described and figured a three-clawed larva of *Calliphari-xenos.* This anomalous condition could not be checked on the poor type material at the United States National Museum.

The Stichotrematidae have a unique arrangement, which has been figured correctly by Hofeneder (1910a) but incorrectly by Pierce (1918). An examination of paratype material at the United States National Museum showed that the front tarsi are pulvilliform, the middle tarsi are short-bristlelike, and the hind tarsi are long-bristlelike (fig. B, 15–17). Pierce figured all three pairs of tarsi as pulvilliform (1918, Pl. 67).

The structure of the head of the first larva has been very unsatisfactorily discussed and figured by previous authors. In an attempt to remedy this situation drawings of *Eoxenos laboulbenei* and *Stichotrema dalla-torreanum* are presented which were made with a camera lucida on an oil immersion microscope. Nevertheless, because of the minute size of the parts, an absolutely correct interpretation is not claimed. There are five ocelli in *Eoxenos,* the usual number in Strepsiptera, but only three in *Stichotrema,* of which the anterior is much the largest. In addition to the ocelli, the head of *Eoxenos* presents on each side a large mediolateral sensorium, behind which are two small bristles and in front of which are two large bristles. It is possible that the larger and anterior of the large bristles represents the antenna, but this is certainly doubtful. A similar picture is presented by *Stichotrema* in dorsal view except that the sensorium is absent and the bristles are relatively smaller. In both genera a large median sclerite can be seen ventrally. It bears a pair of bristles, large and terminal in *Eoxenos* but small and medial in *Stichotrema.* This sclerite probably represents both mentum and submentum, as well as labium. Just anterior to the mentum on each side is a curved sclerite which bears a fleshy palpus. These sclerites are apparently the maxillae. In *Sticho-trema* the maxillary palpus is three- or possibly four-segmented with a long bristle which arises laterally from the third. The palpus of *Eoxenos* could not be seen in lateral view, and only two segments could be distinguished. There is a possibility, however, that it is also three- or four-segmented. Between and

above the anterior ends of the maxillae lies the mouth opening. Mandibles, if present, were not visible.

A graphic representation of the relationships of the various genera is presented (fig. A, 10). It is based on a combination of all the characters given above. There have apparently been four distinct lines of development. As indicated by the three- to two-segmented tarsi of the males and the nonpulvilliform tarsi of the first larvae, the parasites of Homoptera form a distinct, independent group. Another line of evolution is formed by Mengeidae to Stylopidae, in which the male tarsi are five- to four-segmented and the front and middle tarsi of the first larvae are pulvilliform. The Myrmecolacidae appear to be a specialized offshoot of a *Triozocera*-like form in which the fifth tarsal segment has been lost, the eyes and prescutum have become greatly enlarged, and the number of antennal flabellae has been reduced from two to one. This family parasitizes ants and is known only from males. However, the Stichotrematidae, which parasitize various Orthoptera, are known only from females and first larvae. That this may be more than a coincidence is brought out in a recent paper by Hofeneder (1939) in which that author recites the findings of Ogloblin in South America. Ogloblin, in correspondence with Hofeneder, recorded two genera of myrmecolacid males from various ants and two genera of stichotrematid females and young from mantids and gryllids. Furthermore, exuviae of the first larvae in ants were found identical with first larvae taken from stichotrematid females. The obvious conclusion drawn by Ogloblin was that a type of parasitism existed wherein the males parasitized ants and the females attacked Orthoptera. If this extremely peculiar condition can be verified, the Stichotrematidae will become a synonym of the Myrmecolacidae. Until verification it will be safer to treat the two families as heretofore. Branching off somewhere along the same line are the Callipharixenidae, which occur in Amboyna, Siam, and East Africa, with an unverified record from southeastern United States. The male of *Corioxenos* seems most closely related to the American *Triozocera*, but the four-segmented

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FIG. B

1. *Triozocera mexicana* Pierce, male antenna.
2. *Mengenilla santschii* (Pierce), male antenna.
3. *Mengea tertiaria* Grote, male antenna (redrawn after Ulrich).
4. *Eoxenos laboulbenei* Peyerimhoff, male antenna.
5. *E. laboulbenei*, head of first larva, ventral.
6. *E. laboulbenei*, head of first larva, dorsal.
7. *E. laboulbenei*, first larva, ventral.
8. *E. laboulbenei*, first larva, dorsal.
9. *Stichotrema dalla-torreanum* Hofeneder, head of first larva, ventral.
10. *S. dalla-torreanum*, head of first larva, lateral.
11. *S. dalla-torreanum*, maxillary palpus of first larva.
12. *E. laboulbenei*, male aedeagus, lateral.
13. *T. mexicana*, male aedeagus, lateral.
14. *M. santschii*, male aedeagus, lateral.
15. *S. dalla-torreanum*, hind leg of first larva.
16. *S. dalla-torreanum*, middle leg of first larva.
17. *S. dalla-torreanum*, hind leg of first larva.
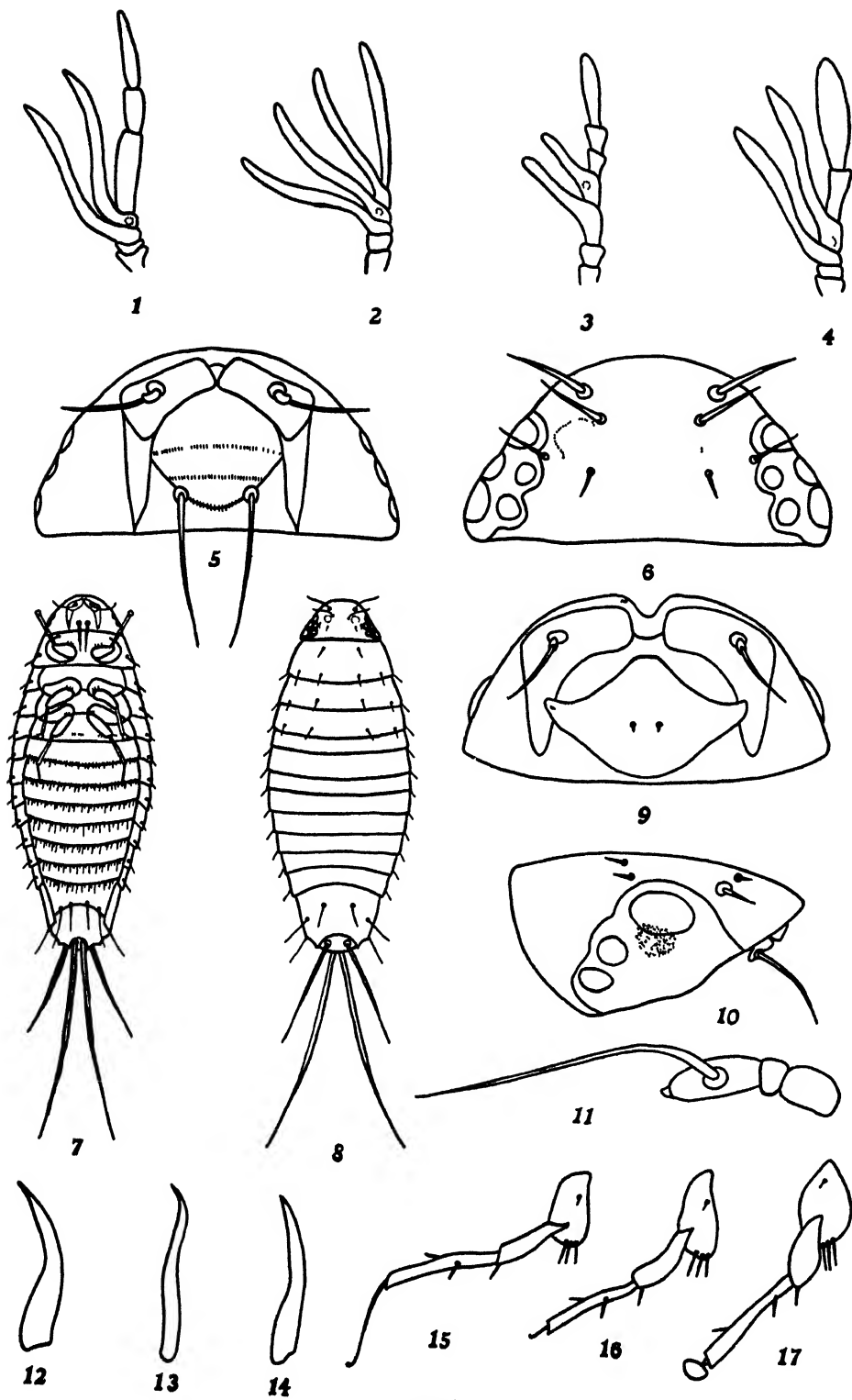
Fig. B.

clawless tarsi, five-segmented antennae, and peculiar female of *Corioxenos* make the relationship somewhat doubtful. For the present, at least, it appears best to derive it along a separate line.

GEOGRAPHICAL DISTRIBUTION AND HOST CORRELATION

Although Strepsiptera have been recorded from all the major zoögeographical regions, the only family thus widespread is that of the Stylopidae. The record of the Halictophagidae is almost as complete since it is unknown only from the Ethiopian region. Furthermore, these two families are well represented throughout their range. Agreeing in this respect, but limited to the Holarctic and Australian regions, are the Elenchidae. However, the remaining families are characterized by a discontinuous or extremely limited distribution. Thus, the Mengeidae have two genera in the Mediterranean area, one of which is also found in Australia, and one genus in the northern Neotropics; the Callipharixenidae occur in the southeastern Oriental region and in British East Africa; the Myrmecolacidae are found in the Oriental and Neotropical regions; and the Stichotrematidae are known from the Australian and Neotropical regions.

Conclusions which can be drawn are that all the families are of ancient origin but only the first three mentioned above are flourishing today. The others, because of their few species and localized occurrence, may be classed as relic families.

It is obvious that the distribution of the various genera is limited to the distribution of the host genera. Also, in most instances the host is more widely distributed than its parasite. The following outline of distribution and host relationships according to genera has been taken partly from the lists of Pierce (1909, 1911a, 1918), Salt and Bequaert (1929), and Ulrich (1930b), together with records heretofore unpublished. New records of hosts or localities are marked with an asterisk.

DISTRIBUTION OF HOST AND PARASITE GENERA

Host Genus	Known Distribution of Parasites	Parasite Genus
Unknown	Eocene fossil in Baltic amber	*Mengea*
Unknown	Mediterranean area, Australia	*Mengenilla*
Unknown	Mediterranean area	*Eoxenos*
Unknown	Northern Neotropics	*Triozocera*
(HYMENOPTERA)		
Pheidole	Northern Neotropics	*Caenocholax*
Formica (?)	Oriental region including *Philippine Islands	*Myrmecolax*
Camponotus	Argentina	⎫
Pseudomyrma	Argentina	⎬ New genus (?)
Solenopsis	Argentina	⎭

Andrena	Holarctic region	*Stylops*
*Conanthalictus	*Southern California	New genus
Halictus	Holarctic region	*Halictoxenos*
Augochlora	Illinois	*Halictoxenos*
Pseudopanurgus	Nearctic region	⎫
Panurginus	Palearctic region	⎬ *Crawfordia*
Panurgus	Palestine	⎭
Halictoides	*Western United States, Austria	*Pseudostylops*
Rhophites	Central Europe	*Pseudostylops* (?)
Paracolletes	Australia	New genus (?)
Hylaeus	Mediterranean area, *Sierra Nevada, California, *Formosa	*Hylecthrus*
Paleaeoriza	Australia	*Hylecthrus* (?)
Nomia (?)	Africa	New genus (?)
Meliturga (?)	Hungary	New genus (?)
Polistes	World-wide except Australia	⎫
Vespa	Palearctic, Oriental regions, Tennessee (?)	⎬ *Xenos*
Mischocyttarus	Nearctic, Neotropical regions	⎭
Polybia	Brazil	*Xenos* (?)
Clypeopolybia	Argentina	*(Clypoxenos)* (?)
Belonogaster	Africa	*Xenos* (?)
*Apoica	*Panama	*Xenos* (?)
Nectarina	Peru	New genus (?)
Paragia	Australia	*Paragioxenos*
Ropalidia	Ethiopian, Oriental regions, including *Philippine Islands	New genus
Psiliglossa	Mediterranean area	New genus (?)
Episyron (?)	Europe	New genus (?)
Dasymutilla (?)	Louisiana	New genus (?)
Odynerus	World-wide except Australia	⎫
Eumenes	Ethiopian, Oriental regions; *Palestine; *Sierra Nevada, California	⎪
Zethus	Southeastern United States, Peru, South Africa	⎪
Sphex	World-wide except Australia	⎬ *Pseudoxenos*
Sceliphron	World-wide except Africa	⎪
Podalonia	Holarctic	⎪
Chlorion	World-wide except Australia	⎪
Tachytes	India, *China	⎪
*Microbembix	*California	⎭
Tachysphex	Algeria	*Pseudoxenos* (?)
Trypoxylon	Mexico	*Pseudoxenos* (?)
Montezumia	Argentina	*Pseudoxenos* (?)
Bembecinus	Mediterranean area, *Philippine Islands	⎫
Bembex	Australia, Louisiana (?)	⎬ *Pseudoxenos* (?)
Stizus	Mediterranean area, Australia	⎭

(ORTHOPTERA)

Sexava	Islands near New Guinea	*Stichotrema*
Gryllotalpa	East Africa	New genus (?)
Acantiothespis	Argentina	New genus (?)
Tridactylus	India	*Tridactylophagus*

(HOMOPTERA)

Cicadella	Oriental, Australian regions	
Oncometopia	Nearctic region	
Diedrocephala	Guatemala	
Deltocephalus	Colorado, Europe, Australia (?)	
Euttetix	Western United States, Australia	
Hecalus	Australia	
Thompsoniella	Ceylon	
Agallia	*California	
Aceratagallia	North America	
Paradorydium	Australia	
Euscelis	*Western Canada	
Athysanella	*Utah	
Draeculacephala	*Mexico, *Washington, D. C.	
Idiocerus	*Washington	*Halictophagus*
Flexamia	*Arizona	
Laevicephalus	*Western Canada	
Latalus	*Western Canada	
Ribautiella	*Western Canada	
Stirellus	*Alabama	
Xerophloea	*Nearctic, Neotropical regions	
Hysteropterum	*Idaho	
Pentagramma	"Dacota"	
Ossoides	Java	
Pyrilla	India	
Otinotus	India	
Polyglypta	*Costa Rica	
Tituria	Hainan Island	
Acucephalus	*Massachusetts	
Phlepsius	*Arizona, Australia	*Halictophagus* (?)
Stegelytra	Germany	
Phenice	Java	
Scolops	*Utah	
Chloriona	Germany	
Pseudoliarus	Germany	Unknown
Stiroma	Germany	
Eurysa	Germany	
Stobaera	Arizona	
Epora	Borneo	Unknown (*Colacina*)
Saccharosydne	Porto Rico	
Dicranotropis	Java	
Delphacodes	*Western Canada, Russia	*Stenocranophilus*
Perkinsiella	Java	
Delphacodes	Australia	
Perkinsiella	Fiji Islands	
Hadeodelphax	Australia (?)	*Elenchus*
Megamelanus	Maryland	
Aloha	Hawaii	
Platybrachys	Australia	

(HETEROPTERA)

Calliphara	Amboyna	*Callipharixenos*
Chrysocoris	Siam	*Callipharixenos*
Antestia	East Africa	*Coriozenos*

INTERNAL ANATOMY

The principal contributors to our general knowledge of the internal organs of these insects are Nassonow (1892), and Smith and Hamm (1914). Work on specific structures has been published by Ulrich (1930a) and Strohm (1910); but the internal anatomy cannot be considered well known. Nassonow's work, though in the main excellent, was incorrect in certain respects and dealt almost entirely with the female. Likewise, although the paper by Smith and Hamm was an admirable contribution, certain points in it are open to question; and their work also dealt only with the female.

According to Nassonow, the nervous system in the two sexes is similar. The brain mass is large, and in the male the optic and olfactory lobes are well developed. There is a single compound ganglionic mass in the thoracic region which gives off five pairs of nerves, of which the last, in the male, are the motor nerves of the hind wings. Another compound ganglion occurs in the region of the third abdominal segment and gives off two pairs of lateral and five pairs of terminal nerves.

The circulatory system is very simple, at least in the female. According to Ulrich (1927b), there is a simple tubelike dorsal heart which possesses nine pairs of ostia. The heart leads anteriorly into the aorta, which reaches into the cephalothorax. The pericardial septum is only weakly developed, and the pericardial cavity is largely filled with fatbody cells.

The respiratory system of the female mengeid apparently consists of a longitudinal pair of tracheal trunks arising from seven pairs of spiracles in the abdomen and probably from a pair each in the mesothorax and metathorax (Parker and Smith, 1933). Endoparasitic females possess only a single pair of metathoracic spiracles and main tracheal trunks, from which one or two pairs of abdominal and a single pair of cephalothoracic tracheae are given off in the region of the first abdominal segment. Two pairs of abdominal branches are found in *Xenos* but only a single pair in *Stylops*. Studies by the author agree on this point with the observations of Smith and Hamm but are at variance with those of Nassonow and Pierce. The cephalothoracic and abdominal trachea may or may not fuse apically to form a complete circle. The possibility of a pair of mesothoracic spiracles in *Callipharixenos* has been previously discussed. The records made by Pierce of abdominal spiracles in *Halictophagus* (= *Dacyrtocara*) females are very doubtful. The author was unable to discover any such structures in the type specimens.

The digestive tract, which ends blindly with the midgut in the first larvae, is complete but strongly reduced in the adults of both sexes. In the female it is merely a straight, undifferentiated, apparently functionless tube. Neither sex takes food by the mouth in the adult stage; there are no Malpighian tubules, and the process of excretion is unknown. Apparently a late endoparasitic stage of Strepsiptera can be considered an unnecessary additional organ of the host. Probably food material is absorbed and products of excretion are eliminated much as in any other organ of the host's abdomen.

The reproductive system of the male consists of a pair of ovoid testes which lead almost directly into an enlarged seminal vesicle and thence through the short ejaculatory duct to the aedeagus. The female mengeid possesses a terminal, abdominal genital opening through which fertilization takes place, but the internal organization is unknown. Endoparasitic females possess median secondary oviducts on the first few abdominal sternites. There are no discrete ovaries since these break up into masses of eggs before the adult stage is reached. The developing embryos lie free in the abdomen, surrounded by blood and fatbody cells. The first larva must burst open the shell of its egg, make its way out through one of the funnel-shaped "oviducts," crawl along the brood passage between the female and its last larval skin, and finally emerge through the opening in the neck region of the puparium.

BIOLOGY

Detailed accounts of the biology of several species have been given by Nassonow (1892), Brues (1903), Pierce (1909), and Schrader (1924). An excellent summary of these and other works is given by Ulrich (1927b).

The life history of a typical strepsipteron is as follows: A host bearing a female parasite is located by a male parasite, which climbs upon it and, by means of a hook-shaped aedeagus, affects copulation for a few seconds with the aperture in the neck region of the female puparium. The actively motile sperm find their way along the brood passage of the female, through the genital tubes, and into the body cavity. Here they fertilize the masses of eggs which have reached the metaphase of the first maturation division. The extrusion of the polar bodies, formation and cleavage of a fusion nucleus, and establishment of a blastula are events of the first three or four hours after copulation (Schrader, 1924). There is only a small amount of yolk in the egg, and during the development of the embryo nourishment is apparently absorbed through the thin-walled chorion. The mature, partially curled-up embryo breaks out of its egg by pressing against the chorion with its sharp head, while at the same time it uncurls. Then it finds its way out through the genital tubes and along the brood passage to the opening which lies just outside the abdomen of the host. The first larva leaps or crawls from the host onto flowers visited by it, or merely jumps to the ground. Its success now depends on its ability and good fortune in finding a nymph or larva of one or several host species. If it is a parasite of Homoptera, it will strive to jump or crawl directly upon a "hopper" nymph; but if it is a parasite of Hymenoptera, it must depend upon the adult of its host species to carry it back to her brood. The fact that a single female produces between one thousand and five thousand young indicates the high reproductive but low survival potentials involved. The first larva burrows into the host through the delicate intersegmental membranes of the latter in one to three hours. Apparently the burrowing is not accomplished by mandibles but by pushing with the sharply edged head. Also, the backward pointing bristles, with which the larva is beset, are undoubtedly of some assistance. The larva quickly molts within the host, and

its second instar is legless and scarabaeiform. The sexes can be distinguished by a difference in appearance of the gonads beginning with the third instar. Seven larval instars are recorded by Nassonow for *Stylops melittae* in addition to the larviform adult stage of the female. The latter remains permanently sealed in her puparium, which is exserted between the abdominal segments of the host. The male forms an exarate pupa within the last larval skin. When mature, it pushes the pupal pellicle to the bottom of the puparium, thrusts off the puparium cap with its mandibles, crawls out upon the body of the host, and immediately flies away. The male usually emerges on a bright day before noon and searches for a female until evening. Only rarely will a male live until the second day after it emerges. The incredible amount of energy it displays probably uses up its store of food material rapidly; and the accumulation of waste products may be an even more important factor in causing death so soon after emergence.

The actions of a male *Pseudoxenos* were observed by the author on May 18, 1936. A parasitized *Sphex breviceps* (Sm.) was captured at Antioch, California, and at seven-thirty in the evening of the same day the puparium cap was removed under a desk lamp. The male, *Pseudoxenos lugubris* (Pierce), promptly emerged by pulling itself out with its front two pairs of legs and immediately flew into the air. It alighted on the author's white shirt, was captured, and put in a glass-covered dish. The insect exhibited marked positive phototropism, always flying toward the side of the dish nearest the desk lamp. Constant activity was maintained, the wings, antennae, and elytra vibrating rapidly. In walking, the middle legs were used principally, the front legs somewhat less, and the hind legs were dragged along behind. Also, when the insect walked, the abdomen displayed a rotary movement and frequently acted as a lever to raise the hind legs from the surface of the glass. Whenever this was accomplished, the insect took flight. Two other *Sphex breviceps* bearing female parasites were introduced into the dish, but neither the hosts nor the male parasite showed any interest in one another. By 10:00 P.M. the male had become less active. It frequently turned over on its back and, while in this position, gyrated rapidly with the head as the center of motion and with the wings fluttering violently. By midnight the quiescent periods had become longer and more accentuated. However, the appendages were constantly twitching at least slightly. The male was dead by 3:00 A.M. the next morning.

. Two days later (May 20) the pupal cap was removed from a puparium in a specimen of *Sphex nasalis* (Prov.). The male within wriggled his antennae but did not seem able to emerge unassisted. At 5:00 P.M. it was withdrawn from the puparium, being removed from the latter with a cutting needle. The male continued to twitch its legs, mouthparts, and antennae, but not its undeveloped wings. The abdomen was occasionally distended and rotated as mentioned above. This movement was apparently a futile attempt to initiate flight by spreading the hind wings and raising the body off the ground. In addition to twitching, the antennae were rhythmically shortened and lengthened by stretching and contracting the membrane between the first segment

and the head proper. All intersegmental membranes were prominent and exhibited pulsatory action. By noon of the next day the only signs of life were the twitching of the antennae, and the opening and closing of the mandibles. By this time the elytra, antennae, and wing veins had become considerably darker. The insect showed no signs of life after 7:00 P.M.

Some notes were also made on the actions of the first larvae of a gravid female *Pseudoxenos lugubris* extracted from *Sphex transversus* Fern. At 10:00 P.M. (September 26) the first larvae were forced out of the brood-passage opening by pressing gently on the female with forceps. The first larvae exhibited in general a positive phototropism, although this was not marked as in the case of *Stylops* triungulins. Their course toward the lamp was often zigzag, and occasionally one would turn with a single motion at right angles or even face directly away from the light. At intervals the terminal stylets were folded beneath the body, and the insect leaped a distance of five to ten millimeters. The average speed of a specimen traveling toward a light was five millimeters (or about twenty times its own length) a minute. Some of the triungulins lived as long as eight days in a cardboard box. Although they crawled freely over the bodies of two *Odynerus* larvae, they made no attempt to enter them.

Among the phenomena which have been ascribed to the Strepsiptera are parthenogenesis and polyembryony. The arguments for and against parthenogenesis are most fully presented by Pierce (1918). The rarity of males in certain genera, such as *Halictoxenos,* is the main argument for parthenogenesis. The work of Schrader (1924) on *Xenos peckii* Kirby (=*Achroschismus wheeleri* Pierce) indicates that fertilization is the rule in that species. Also, parasite records tend to discount the general application of the theory. Pierce lists a total of 1,318 males to 634 females, a compilation from records in all families. To this the author can add the following summarized records: *Polistes fuscatus aurifer* Sauss., 1,929 wasps containing 26 males or male exuviae and 157 females; *Sphex nasalis* (Prov.), *craspedotus* Fern., *aberti* (Hald.), *arvensis* (Dahl.), and *breviceps* (Sm.), 218 wasps containing 73 males or male exuviae and 70 females; *Andrena complexa* Vier., 520 bees containing 124 males or male exuviae and 146 females; *Delphacodes consimilis* (Van Duzee), 5,569 "hoppers" containing 36 males or male exuviae and 10 females. The *Polistes* record, which was made from hibernating wasps, shows a very small percentage of males. However, in this species only female *Xenos* overwinter, with rare exceptions, and collections made in the summer give at least as many male parasites as female. The evidence for parthenogenesis is weak and, if it occurs at all, it is probably limited to a few of the genera parasitic on bees.

Polyembryony has been recorded for *Halictoxenos* by Noskiewicz and Poluszynski (1924*a*). From their account, which is short and incomplete, it appears that in the first stage of polyembryony the blastoderm divides into several vesicles. In the following stage the embryos are formed by the invagination of the cells of the vesicles toward the center. The number of vesicles varies from one to several. The number of embryos formed by an egg cannot

be less than two, but may be as many as forty. Whether or not polyembryony is found in other Strepsiptera is unknown.

It was early recognized that stylopization produced changes in appearance of the host. This change is of varying extent in different individuals and is not evident at all in some groups. The first fairly complete treatment of the subject was by Jean Perez (1886). A summary of this work and additional information on the subject are contained in the papers of Pierce (1909, 1918). Smith and Hamm (1914) also contributed to the subject. The most comprehensive treatment, however, was given by Salt (1927a). According to the latter, the results of the stylopization in *Andrena* are, in general, reduction in size of head, enlargement of abdomen, a disturbance in wing venation, and various changes in puncturation and pubescence. In the female, he cites the reduction of pollinigerous organs, loss of anal fimbria, changes in relative lengths of antennal segments, acquisition of angular cheeks, reduction of facial foveae, lightening of color of the ventral abdominal pubescence, assumption of yellow on the clypeus, and some diminution in the size of the sting and its accessories. For the male he records the development of long hairs resembling the female flocculi, widening of the posterior basitarsus, acquisition of anal fimbria, changes in the proportionate lengths of antennal segments, loss of the angle from the cheeks, development to some extent of facial foveae, assumption of a black clypeus, and a reduction in the size of external genitalia. It should be emphasized that not all the characters listed above occur in any one specimen. From the author's own experience it can be said that there is usually a diminution of the head, a change in puncturation and pubescence, and a tendency to converge with respect to secondary sex characters. Fewer alterations as a result of stylopization are produced in other solitary Hymenoptera, and in social Hymenoptera and Homoptera little change occurs. The alteration of wing venation in leafhoppers described and figured by Pierce (1918) is probably merely the result of coincidence since the venation of unstylopized specimens is often highly unstable.

Salt regards the alteration of secondary sex characters as the result of an upset in the nutritional balance of the host which affects the reaction of the sexual hormones and produces intersexes in the sense of Goldschmidt. Also capable of explanation on a nutritional basis is the fact that those stylopized larvae which have a fixed amount of food in a closed cell (i.e., solitary Hymenoptera) emerge earlier than unstylopized specimens, whereas those which are progressive feeders as larvae (social Hymenoptera), when stylopized, emerge later than is normal. It would seem that the former finish their food and emerge early owing to drains on their sustenance by the parasites. The social wasps, however, continue to feed for a longer than normal time as larvae to make up for loss to the parasites.

As would be expected under the circumstances, the alteration of external characters of *Andrena* has given rise to much confusion in the taxonomy of the group. Many species described from stylopized specimens were later found to be synonyms. A list of such species is given by Perkins (1918). However,

Linsley (1937) has recorded an instance in which a stylopized intersex of *Andrena porterae* Ckll. was of value in associating the sexes of this strongly dimorphic species.

Effects on internal organs are also pronounced. Stylopized female hosts usually have the ovaries reduced to the point of obsolescence; in Hymenoptera the air sacs are more or less crowded; and in the male the testes are reduced in size but usually functional.

It might be expected that the longevity of stylopized specimens would be seriously impaired. This is undoubtedly so when the parasite is a male which on emergence leaves a gaping hole accessible to drying effects and fungus. But the female strepsipteron has apparently reached an almost perfect state of parasitism and hardly shortens the life of its host. This is probably because the host has less tissue of its own for which it must provide food, and thus the insidious draining of material from its blood may be no more depleting than the demands of the supplanted organs.

ECONOMIC SIGNIFICANCE

Approximately one hundred genera of hosts have been recorded for the Strepsiptera. Of these, over fifty contain species which are potential enemies of agriculture. The effect of stylopization on beneficial pollinators or predators is difficult to evaluate. In fact, the importance of wild bees in pollination is doubtful in many instances. Furthermore, the degree of parasitism is usually low, rarely exceeding 50 per cent. The situation with respect to leafhoppers is more definite. According to Misra (1916), halictophagids are a definite factor in the control of sugar-cane leafhoppers of the genus *Pyrilla*. A similar control is noted with respect to the sugar-cane leafhopper, *Saccharosydne saccharivorus* (Westw.), stylopized by *Stenocranophilus*.

It is doubtful whether Strepsiptera will ever be the chief factor controlling the abundance of their hosts. However, 10- or 20-per cent parasitism may be the necessary addition to the environmental resistance which will effect control.

TAXONOMY

The problem of host specificity is a vital one in the taxonomy of the Strepsiptera. If, as has been suggested, every parasite species is limited to a single species of host, the classification of the group resolves itself largely into the determination of host species. In the author's opinion, however, species of Strepsiptera are not absolutely specific. One species is often found on several related host species or sometimes on different host genera. The correlation of host with parasite in British *Andrena* by Perkins (1918) is in accordance with this opinion. The degree of specificity in the parasites of Hymenoptera is fairly high, but the parasites of Homoptera do not follow this rule. A single species of the latter may infest several host genera, and the genus *Halictophagus* attacks Fulgoridae, Cicadellidae, and Membracidae whereas the closely related genus, *Tridactylophagus*, is found on Orthoptera. It is therefore essential that the taxonomy of the Strepsiptera should stand on its own merits

and not upon host correlation. The author has attempted to further this aim by emphasizing structural characters in the adults and first larvae.

Generic characters in the male are the number of segments in the antennae, structure of the mouthparts and eyes, form of the thorax and legs, wing venation, and shape of the aedeagus. In the female the number of genital tubes, degree of fusion of the cephalothorax, form of the mandibles, and proportions of the cephalothorax are important. The first larvae rarely exhibit specific differences, but the prominence of the mouthparts and ocelli, form of the legs, and spininess of the body are of excellent generic value. Although males are relatively simple to separate into species, females present a much more difficult problem. Slight and variable differences in coloration and proportions of the cephalothorax, and the shape of the mandibles and brood-passage opening are the main diagnostic characters. The variation between individuals of a single species makes determination feasible only from a series of specimens, as far as the females are concerned.

KEY TO THE FAMILIES AND GENERA OF STREPSIPTERA

MALES

1. Tarsi five-segmented and clawed...................(Mengeidae).................2
   Tarsi fewer than five-segmented and clawless....................................5

2. Antennae seven-segmented, third and fourth segments laterally flabellate...........3
   Antennae six-segmented...4

3. Fifth antennal segment elongate, longer than the sixth and seventh together; postlumbium short and linear; first vannal vein about half as long as second vannal; fourth tarsal segment bilobed, the others linear................*Triozocera*
   Fifth antennal segment not longer than the sixth; postlumbium oval; first vannal vein reaching almost to the wing margin; fourth tarsal segment linear ....*Mengea*

4. Third and fourth antennal segments laterally flabellate...................*Eoxenos*
   Third to sixth antennal segments laterally flabellate....................*Mengenilla*

5. Tarsi four-segmented..6
   Tarsi three- to two-segmented..14

6. Antennae seven-segmented, the fourth very short, fifth to seventh very long .... (Myrmecolacidae) 7
   Antennae fewer than seven-segmented.......................................8

7. Hind wing with two detached veins between the radius and media, cubitus present; maxillary palpus slender but not long filiform...............*Myrmecolax*
   Hind wing with one detached vein between the radius and media, cubitus absent; palpus long filiform.....................................*Caenocholax*

8. Third and fourth antennal segments laterally flabellate, antennae five-segmented; first tarsal segment subequal in length to the following three segments together; postlumbium short and linear........................
   (Callipharixenidae) ....*Corioxenos*
   Third antennal segment only, laterally flabellate; first tarsal segment much shorter than the following three segments together........(Stylopidae)........9

9. Antennae six-segmented; postlumbium oval or semicircular.................*Stylops*
   Antennae fewer than six-segmented..10

10. Antennae five-segmented, the fourth very short.........................*Hylecthrus*
    Antennae four-segmented, third and fourth subequal......................11

11. Postlumbium oval or semicircular; radius of hind wing unbroken..................12
    Postlumbian short, not oval, often somewhat spindle-shaped; radius ending
      near the middle of the wing..13
12. With two detached veins between radius and cubitus..................*Halictoxenos*
    With no detached veins between radius and cubitus...................*Crawfordia*
13. Detached radial sector originating only slightly behind the end of the radius
      proper..*Xenos*
    Detached radial sector originating well behind the end of the radius proper
      ....*Pseudoxenos*
14. Tarsi two-segmented; antennae four-segmented, third segment laterally flabel-
      late, flabellate portion originating at the base of the segment..........
      (Elenchidae) ....*Elenchus*
    Tarsi three-segmented, antennae seven-segmented........(Halictophagidae)......15
15. Third antennal segment only, laterally flabellate..................*Tridactylophagus*
    Third and at least fourth antennal segments laterally flabellate.................16
16. Antennae compact, the segments short............................*Halictophagus*
    Antennae not compact, some of the segments three or more times as long as
      broad...*Stenocranophilus*

<center>FEMALES</center>

1. Adult stage free-living, with legs, antennae, and eyes........(Mengeidae)........2
   Adult stage partially endoparasitic, without legs, antennae, or eyes...............3
2. Antennae five-segmented..*Eoxenos*
   Antennae four-segmented...*Mengenilla*
3. Cephalothorax with hooklike projections behind spiracles, parasites of Orthop-
      tera ....(Stichotrematidae).....................*Stichotrema*[1]
   Cephalothorax without such projections...................................4
4. Cephalothorax greatly elongate, with two pairs of spiracles, or with the head
      and thoracic segments distinct, parasites of Heteroptera...(Callipharixenidae)...5
   Cephalothorax with a single pair of spiracles, thoracic segments not well defined.....6
5. Cephalothorax with two pairs of spiracles, abdomen with five genital tubes,
      parasites of Scutellaridae.....................................*Callipharixenos*
   Cephalothorax with one pair of spiracles, abdomen with four genital tubes,
      parasites of Pentatomidae...*Corioxenos*
6. Parasites of Hymenoptera.....................(Stylopidae)....................7
   Parasites of Homoptera or Gryllidae..13
7. Abdomen with five genital tubes...8
   Abdomen with fewer than five genital tubes................................10
8. Head completely fused to the thorax so that the brood-canal opening does not
      reach the lateral margins; parasites of Halictidae..................*Halictoxenos*
   Extensions from the brood-canal opening reaching to, or almost to, the lateral margins..9
9. Cephalothorax with the width at the base of the mandibles three-fifths and the
      width at the base of the head four-fifths the breadth at the spiracles; para-
      sites of Dufoureidae..*Pseudostylops*
   Cephalothorax with the width at the base of the mandibles about two-fifths
      and the width at the base of the head about three-fifths the breadth at the
      spiracles; parasites of Andrenidae..................................*Stylops*
10. Abdomen with four genital tubes; parasites of Vespidae..................*Xenos*
    Abdomen with three or two genital tubes.................................11

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[1] Note the possibility previously mentioned that Stichotrematidae may represent females
of Myrmecolacidae.

11. Abdomen with two genital tubes; parasites of Hylaeidae.................*Hylecthrus*
    Abdomen with three genital tubes...12
12. Cephalothorax with a broad, dark, basal band; parasites of Panurgidae....*Crawfordia*
    Cephalothorax without a broad, dark, basal band; parasites of Vespidae and
    Sphecidae ....*Pseudoxenos*
13. Brood-passage opening a narrow, linear or oblong slit; thorax prominent;
    (Halictophagidae):
    Parasites of Gryllidae..*Tridactylophagus*
    Parasites of Homoptera...*Halictophagus*
    Parasites of Fulgoridae..*Stenocranophilus*
    Brood-passage opening broad and semicircular, thorax reduced and ringlike
    in back of brood-passage opening; parasites of Fulgoridae..(Elenchidae)..*Elenchus*

FIRST LARVAE

1. Front and middle tarsi pulvilliform, hind tarsi setiform.........................2
   Middle tarsi setiform...9
2. Head with two long backward-projecting spines arising near the posterior
      margin ventrally...3
   Head without long spines as above; parasites of Sphecoidea, Vespoidea, and
      Apoidea ....(Stylopidae).........................5
3. Sternites of abdomen with dentate posterior margins but without definite
      bristles; parasites of Heteroptera.........(Callipharixenidae).........*Corioxenos*
   Sternites of abdomen margined posteriorly with bristles........................4
4. All tarsi setiform; parasites of Fulgoridae........ (Elenchidae).........*Elenchus*
   Front and middle tarsi pulvilliform.............(Mengeidae).............*Eoxenos*
5. Tenth tergite with a pair of lateral spines which are about half as long as the
      terminal stylets, ninth sternite bearing a pair of lateral tubercles with long
      apical bristles, front and middle tarsi round, padlike; parasites of Vespoidea
      and Sphecoidea...6
   Tenth tergite without such spines, ninth sternite without tubercles, front and
      middle tarsi slender, padlike; parasites of Apoidea...........................7
6. Bristles of sternites less than half the length of the sternites; parasites of
      social Vespidae ....*Xenos*
   Bristles of sternites more than half the length of the sternites; parasites of
      Eumeninae and Sphecidae..*Pseudoxenos*
7. Abdominal tergites with a row of small sublateral bristles, ninth segment with
      a pair of stout latero-apical setae; parasites of *Halictoides*..........*Pseudostylops*
   Abdominal tergites without a row of sublateral bristles, ninth segment with a
      pair of slender latero-apical bristles..8
8. Abdominal tergites fringed with minute bristles, which are much less than half
      the length of the tergites, hind tarsi short setiform; parasites of *Hylaeus*..*Hylecthrus*
   Abdominal tergites fringed with bristles of two sizes, the longer of which are
      more than half the length of the tergites, hind tarsi long setiform:
      Parasites of Andrenidae..*Stylops*
      Parasites of Halictidae...*Halictoxenos*
9. Front tarsi pulvilliform, middle tarsi short setiform; parasites of Orthoptera
      .... (Stichotrematidae) ....*Stichotrema*
   All tarsi long setiform (Halictophagidae):
      Parasites of Homoptera.......................................*Halictophagus*
      Parasites of Fulgoridae.......................................*Stenocranophilus*
      Parasites of Gryllidae..*Tridactylophagus*

ORDER STREPSIPTERA Kirby

Strepsiptera Kirby, 1813.
Phthiromyae Latreille, 1809.
Rhipidoptera Lamarck, 1816.
Rhipiptera Latreille, 1817.
Stylopites Newman, 1841.
Stylopides Lacordaire, 1859.
Stylopinae Lameere, 1900.
Xenidae Semenov, 1902.
Stylopidae, authors.

Family MENGEIDAE Pierce

Mengeidae Pierce, 1908:76, 1911a, 1911b, 1918.
Mengeoidea Pierce, 1908:76, 1911a, 1911b, 1918.
Mengenillidae Hofeneder, 1910a.
Mengeidae, Ulrich, 1930:11.

The family readily separates into four genera, easily distinguished by the antennae of the males (fig. B, 1–4). Of these, *Mengea* is known only from a single male Tertiary fossil in German Baltic amber. It is beautifully preserved and has been completely described and figured by Ulrich (1927a). Its similarity to *Eoxenos*, which inhabits the same region today, is remarkable. The latter differs principally in its somewhat more specialized antennae and wing venation.

The most primitive of unspecialized Strepsiptera are included in the Mengeidae. The mature females are free-living, and both sexes have tarsi with terminal claws. The aedeagus of the male is not hooked, and this circumstance seems correlated with the more usual type of copulation as contrasted with this process in most forms with partially endoparasitic females. Since the early stages, with the exception of the first larva, are unknown, so also are the hosts. It is possible that mengeids may not be endoparasitic in any stage; they may be parasitic in the same way as meloid beetles which live on the egg masses or stored food of their hosts. One point in favor of this idea is the fact that mengeid puparia and the later larval stages of both sexes are found free of the hosts whereas in all other Strepsiptera these are endoparasitic. The free-living females and puparia have been found under stones and on tree stumps in the Mediterranean area.

Genus *Mengea* Grote
(Genotype *Mengea tertiaria* Grote)

Triaena Menge, 1866:3 (nec Hübner, 1816).
Mengea Grote, 1866:100.
Mengea, Pierce, 1908:77, 1909:84, 1911b:3, 1918:424.
Mengea, Ulrich, 1927a:45, 1930b:11.

Genus *Mengenilla* Hofeneder
(Genotype *Mengenilla chobauti* Hofeneder)

Mengenilla Hofeneder, 1910a.
Austrostylops Lea, 1910:514.
Mengenilla, Pierce, 1911a:491, 1911b:10, 1918:427.

Tetrozocera Pierce, 1918:428.
Austrostylops, Pierce, 1918:428.
Mengenillopsis Hofeneder, 1926:56, 1928:195.
Mengenilla, Ulrich, 1930*b*:12.
Mengenillopsis, Ulrich, 1930*b*:12.

The generic identity of *Tetrozocera* and *Mengenilla* has been pointed out by Silvestri (1935). The form of the thorax of the former is somewhat different, but the range of difference is no greater than that found within the genus *Stylops*. *Mengenillopsis* was erected by Hofeneder for a species with no trace of labrum or labium. However, the extremely rudimentary condition of these organs in typical *Mengenilla* makes their absence of little importance. The general similarity of the other mouthparts, antennae, thoracic structure, wing venation, and aedeagus do not seem to warrant generic separation. As herein redefined the genus contains six species, five in the Mediterranean area and one in Australia.

Genus *Eoxenos* Peyerimhoff
(Genotype *Eoxenos laboulbenei* Peyerimhoff)

Eoxenos Peyerimhoff, 1919:171.
Iberoxenos Bolívar y Pieltain, 1926:6.
Eoxenos, Ulrich, 1930:13.
Eoxenos, Parker and Smith, 1933:218, 1934:468.

The morphology and habits of this genus have been described in detail by Parker and Smith (1933, 1934). As they suggested, it is probable that their species and *primitivus* Bolívar y Pieltain are synonymous with *laboulbenei*, in which event only one species of *Eoxenos* is known. It is limited to the Mediterranean area.

Genus *Triozocera* Pierce
(Genotype *Trioxocera mexicana* Pierce)

Trioxocera Pierce, 1909:86.
Triozocera Pierce, 1911*a*:490, 1911*b*:8, 1918:424.
Triozocera, Int. Com. Zoöl. Nom., 1911, Smiths. Inst. Publ. 2013:84.

Although the antennae are seven-segmented and in this respect more primitive than in either *Eoxenos* or *Mengenilla*, the single cubital vein of the hind wing, large postscutellum, lobate fourth tarsal segment, and reduced mandibles indicate that *Triozocera* is the most specialized genus of its family. The single species is known only from males taken at light in Texas and Mexico.

Triozocera mexicana Pierce
(Pl. 3, *a*; fig. A, 9; fig. B, 1)

Trioxocera mexicana Pierce, 1909:86, 1918:427 (holotype, USNM).
Triozocera texana Pierce, 1911*a*:491, 1918:425 (holotype, USNM).

The characters of *mexicana* have been described in a general way in previous parts of this paper under the genus name. Its appearance from dorsal view is illustrated (Pl. 3, *a*). The above synonymy was decided upon after an examination of the types at the United States National Museum. The key

characters given by Pierce (1918) are based on artifact resulting from the mounting technique.

Distribution.—Males, Cordoba, Vera Cruz, Mexico, A. Fenyes (several topotype specimens in the Fenyes collection at the California Academy of Sciences); male, Victoria, Texas, July 4, 1908, J. D. Mitchell.

Family MYRMECOLACIDAE Saunders

Myrmecolacides Saunders, 1872:20.
Myrmecolacidae Pierce, 1908:76, 1909, 1911*a*, 1911*b*, 1918.

The possibility that the ant-parasitic Myrmecolacidae may represent the males of the Orthoptera–parasitic Stichotrematidae has been suggested by Hofeneder (1939). This unusual situation has been discussed on page 102.

According to Hofeneder (1939) the researches of Ogloblin in Argentina have exposed four genera of myrmecolacids, two of which are undescribed. These are *Myrmecolax* on *Solenopis*, *Caenocholax* on *Pheidole*, and two unnamed genera on *Camponotus* and *Pseudomyrma*, respectively. *Caenocholax* had previously been known only from males taken at light in Mexico.

The family contains three or four species characterized by their greatly developed eyes, reduced mouthparts, elongate seven-segmented antennae, and prominent prescutum.

Genus *Myrmecolax* Westwood
(Genotype *Myrmecolax nietneri* Westwood)

Myrmecolax Westwood, 1858:418.
Myrmecolax, Saunders, 1872:34.
Myrmecolax, Pierce, 1908:77, 1909:88, 1911*b*:13, 1918:433.
Parastylops Meijere, 1908:185, 1911:255.
Parastylops, Pierce, 1909:111, 1911*b*:17, 1918:434.

FIG. C

1. *Caenocholax fenyesi* Pierce, hind wing.
2. *C. fenyesi,* maxillary palpus.
3. *C. fenyesi,* aedeagus, posterior view.
4. *C. fenyesi,* aedeagus, lateral.
5. *Myrmecolax philippinensis* Bohart, head and thorax, dorsal.
6. *M. philippinensis,* maxillary palpus.
7. *M. philippinensis,* aedeagus, lateral.
8. *M. philippinensis,* lateral view.
9. *Hylecthrus californicus* Bohart, female cephalothorax, ventral.
10. *Hy. californicus,* female mandible.
11. *Halictoxenos crawfordi* Pierce, female cephalothorax, ventral.
12. *Ha. crawfordi,* female mandible.
13. *Stylops leechi* Bohart, female cephalothorax, ventral.
14. *S. leechi,* female mandible.
15. *Crawfordia pulvinipes* Pierce, female cephalothorax, ventral.
16. *C. pulvinipes,* female mandible.
17. *Pseudostylops desertorum* Bohart, female cephalothorax, ventral.
18. *P. desertorum,* female mandible.
19. *Hy. californicus,* first larva, dorsal.
20. *Hy. californicus,* first larva, ventral.
21. *Ha. crawfordi,* first larva, dorsal.
22. *Stylops pacifica* Bohart, first larva, dorsal.
23. *P. desertorum,* first larva, dorsal.
24. *P. desertorum,* first larva, ventral.
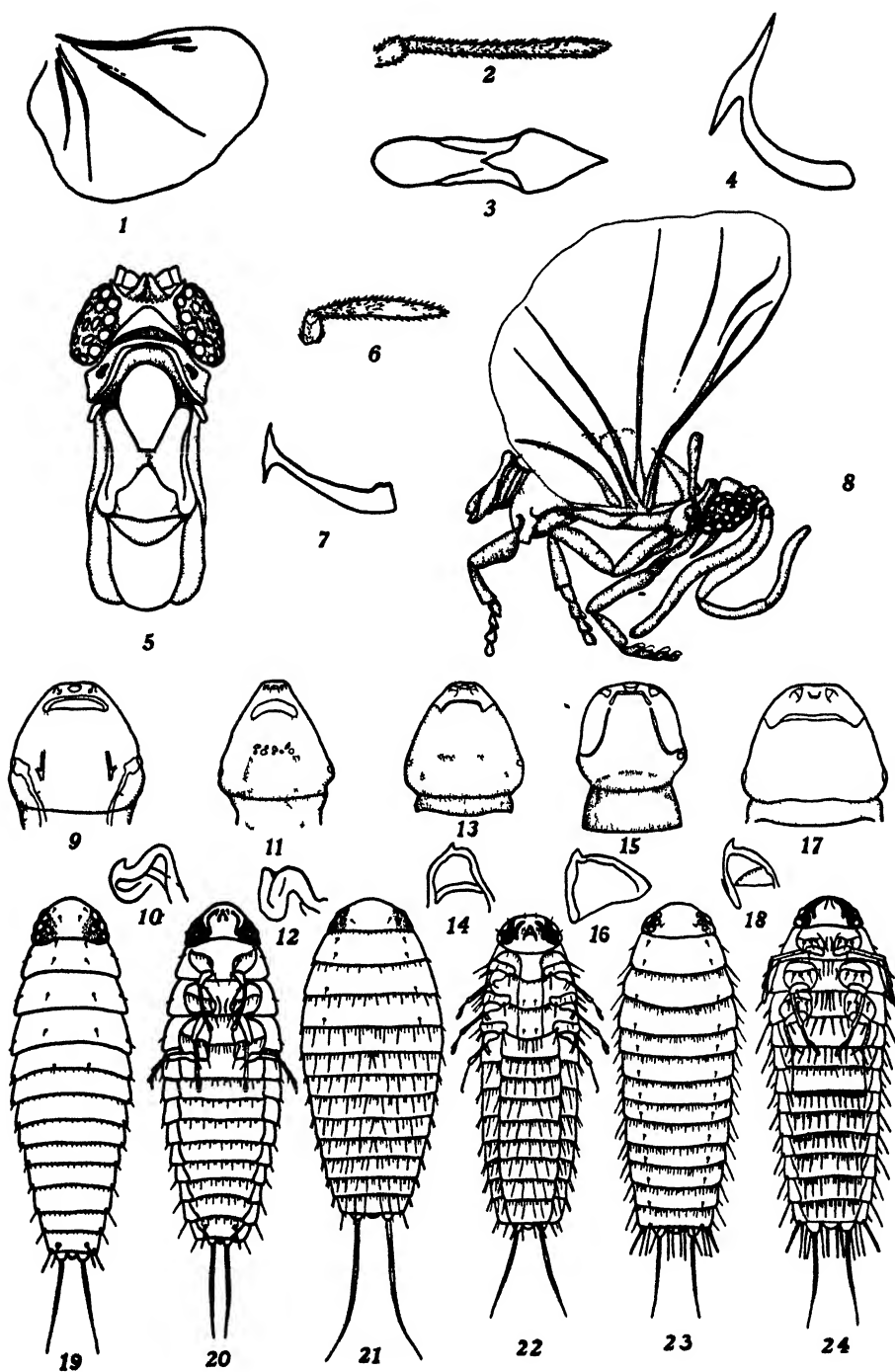
Fig. C.

Myrmecolax nietneri apparently ranges over much of the Oriental region. There seems little doubt that *Parastylops* is synonymous with *Myrmecolax*. The former was placed by Pierce in the Stylopidae on the basis of Meijere's erroneous description of the antennae (1908). Meijere corrected the error in 1911, but Pierce failed to take note of the fact in his later publications.

Myrmecolax philippinensis Bohart, n. sp.
(Fig. C, 5–8)

This is the only species of the genus thus far recorded from the Philippine Islands. It differs from *flagellatus* (Meij.) and *nietneri* Westw. by the entirely different shape of the scutellum; in *philippinensis* it is narrowed anteriorly and with undulate margins. Furthermore, the postscutellum is shorter and stouter than in the other two species. The wing venation differs in some respects from that in Meijere's drawing, but the latter may not be accurate.

Description.—Male. Fuscous, tarsi lighter, wings fumose. Head broader than the thorax; eyes very large; antennae about as long as the thorax, segments three to seven with the length ratio 35:2:18:14:17; mandibles not visible; second segment of maxillary palpus about five times as long as broad, sharply pointed. Prothorax pushed forward into the head. Mesothorax strongly arcuate as seen from above, elytron slightly longer than the sixth antennal segment. Metathoracic prescutum roughly oval, almost twice as long as broad, narrowly truncate behind; scutum with a narrow but distinct median bridge; scutellum narrowly rounded in front, lateral margins undulate, hardly broader than long; post-scutellum short and stout. Aedeagus slender, the main axis two and a half times as long as the apical margin. Length, excluding antennae, 2.0 mm.; length of antennae, 1.8 mm.

Holotype, male, Nupol Makar Cotabato, Mindanao, Philippine Islands, May, 1932, F. Rivera, collector. Holotype borrowed from and to be deposited in United States National Museum.

Genus *Caenocholax* Pierce
(Genotype *Caenocholax fenyesi* Pierce)

Caenocholax Pierce, 1909:88, 1911b:13, 1918:433.

Caenocholax fenyesi Pierce
(Fig. C, 1–4)

Caenocholax fenyesi Pierce, 1909:89, 1911b:13, 1918:433 (holotype, USNM).

The original series of this species was collected by A. Fenyes, who took a number of males at light in Cordoba, Mexico. In addition to the type series at the United States National Museum, a part of the original series is in the Fenyes collection at the California Academy of Sciences. The following is a condensed redescription of the species.

Description.—Eyes composed of approximately twenty large facets; antenna as long as the entire body, first four segments very short, the third with a very long lateral flabellum which reaches about to the middle of the seventh, fourth with a large sensorium, fifth to seventh elongate; maxillary palpus with a small basal segment, terminal segment styletlike. Front and middle coxae as long as the femora, basal tarsal segment stouter than the three following; metathoracic prescutum about twice as long as the triangular scutellum; post-lumbium transversely linear; postscutellum short, no longer than the prescutum; hypoepimera greatly inflated; wing with radius, media, and two anal veins, media broken near the

base, a short, detached piece of vein near apex of radius. Ninth tergite produced backward, covering the genital cavity; aedeagus robust, hook-shaped, compressed dorsoventrally.

Distribution.—Males, Vera Cruz, Cordoba, Mexico, May 21, 1908; male, dead in banana trash on boat from Panama, January 3, 1935, San Francisco, California (in USNM); males, Misiones, Argentina.

Family CALLIPHARIXENIDAE Pierce

Callipharixenidae Pierce, 1918:431.
Callipharixenidae, Blair, 1936:116.

The disparity between the figures of the first larvae of *Callipharixenos* as given by Pierce (1918) and that of *Corioxenos* as given by Blair (1936) may indicate that the family as herein constituted is not a phylogenetic unit. According to Pierce, the tarsus of *Callipharixenos* triungulins is "one jointed, terminated apparently by three slender filaments." The front and middle tarsi of *Corioxenos* first larvae are padlike, and the hind tarsus is setiform. The condition of the type material of *Callipharixenos* at the United States National Museum was such that the author could not see the tarsi of the first larvae. The close relationship of the hosts (Pentatomidae and Scutellaridae) and the similarity of the females make it convenient to place the two genera in one family, at least until *Callipharixenos* is more satisfactorily known.

Genus *Callipharixenos* Pierce
(Genotype *Callipharixenos muiri* Pierce)

Callipharixenos Pierce, 1918:432.
Chrysocorixenos Pierce, 1918:432.
Callipharixenos, Blair, 1936:117.

Chrysocorixenos siamensis Pierce is possibly distinct specifically from *Callipharixenos muiri*. The types of both are characteristically asymmetrical and not as illustrated by Pierce (1918). The former was collected on the scutellarid genus *Chrysocoris* in Siam, and the latter on *Calliphara* in Amboyna.

Genus *Corioxenos* Blair
(Genotype *Corioxenos antestiae* Blair)

Corioxenos Blair, 1936:113.

The single species of the genus has been recorded from the Tanganyika Territory on the pentatomid bug, *Antestia*. An interesting account of the color vision of the first larva has been given by Kirkpatrick (1936).

From the drawing by Blair of the cephalothorax of the female of *Corioxenos,* the head and separate thoracic segments appear to be well marked off. This condition and the unhooked aedeagus of the male indicate less specialization than in the Stylopidae or Halictophagidae.

Family STICHOTREMATIDAE Hofeneder

Stichotrematoidea Hofeneder, 1910b:49.
Stichotrematidae Hofeneder, 1910b:49.
Stichotrematoidea, Pierce, 1911a:503, 1911b:32, 1918:429.
Stichotrematidae, Pierce, 1911a:503, 1911b:32, 1918:429.

Genus *Stichotrema* Hofeneder

Stichotrema Hofeneder, 1910*b*:47.

The family and genus are represented by a single described species from Schouten and Pack islands in Dutch New Guinea where females and first larvae were taken on the tettigoniid, *Sexava*. Their characters have already been summarized. According to Hofeneder (1939), Ogloblin has discovered two genera of stichotrematids parasitic on mantids and crickets in Argentina. The possibility that the Stichotrematidae may represent females of the Myrmecolacidae has been previously discussed, (page 102).

Family STYLOPIDAE Kirby

Stylopidae Kirby, 1813:100.
Xenides Saunders, 1872:20.
Pseudoxenides Saunders, 1872:20.
Stylopinae Perkins, 1905:98.
Xenidae, Pierce, 1908:78, 1909:115, 1911*a*, 1911*b*, 1918.
Halictoxeninae Pierce, 1908:82, 1909, 1911*a*, 1911*b*, 1918.
Hylechthridae Pierce, 1908:78, 1909:113, 1911*b*:18.
Hylecthridae Pierce, 1918:457.
Crawfordinae Pierce, 1908:78, 1909, 1911*a*, 1911*b*, 1918.
Stylopidae, Pierce, 1908:77.
Stylopinae, Ulrich, 1930*b*:13.

In number of host genera parasitized the Stylopidae are approximately equal to the Halictophagidae. Together the two families comprise over three-quarters of the Strepsiptera. The family was broken up by Pierce into Hylecthridae, Stylopidae, and Xenidae, and placed with the Myrmecolacidae in the superfamily Xenoidea. The latter corresponds to the Stylopidae as discussed in the present paper, with the omission of the Myrmecolacidae.

The principal characters of the family are the expanded, four-segmented tarsi, the small prescutum, and the elongate postscutellum. The family divides fairly naturally into two groups, one parasitic on vespoid and sphecoid wasps, and the other on bees. The genus *Hylecthrus,* although belonging to the latter group, is somewhat intermediate.

As can be seen by referring to the host-parasite correlation chart, there is a large number of host genera the parasites of which have been merely recorded or described so incompletely that their affinities are doubtful. In this latter class falls the genus *Paragioxenos* on masarids. A single female specimen of *Paragioxenos* from *Paragia smithii* Sauss. (=*tricolor* Sm.) from Angus, Australia was given the author by J. Bequaert. It resembles *Xenos* except for certain details. The genital tubes were not visible, but these have been recorded as four in number by Hofeneder. Ogloblin's figure of the male (1923) is not clear with respect to wing venation, and this may be a means of differentiation. Likewise the postlumbium is figured as broadly lens-shaped as compared with the rectangular or spindle-shaped appearance in *Xenos*. The female specimen in the author's collection has a peculiar semicircular median

thickening on the ventral prothoracic region. Also the head appears distinct at its base from the thorax ventrally.

Genus *Stylops* Kirby

Stylops Kirby, 1802:112.
Neostylops Pierce, 1918:455.
Katastylops Pierce, 1918:455.
Prostylops Pierce, 1918:455.
Stylops, authors.

Seventy species of this genus have so far been designated. Forty-eight of these are North American and the rest are Palearctic. The majority of the former were named by Pierce, who unfortunately did his work under the impression that *Stylops* were absolutely specific. In many instances, however, this is not so, and a certain amount of synonymy has resulted. Furthermore, a large number of Pierce's species are based on single female specimens from which it is often impossible to formulate a specific concept. Certain outstanding species can be readily determined from the female, but usually a series of specimens is required. The males of these "difficult" species may be very easy to distinguish. For these reasons the author has made synonyms only where distinctive species are concerned, and the uncertain forms have been placed in a group by themselves. The present state of knowledge makes it inadvisable to give a key to the females, but diagnoses and figures are given of many of the species. These are based on an examination of the types by the author, unless otherwise stated. The drawings of the female cephalothoraces in figures D and E were made with a camera lucida and, since their asymmetry is characteristic, it has not been corrected.

The status of *Neostylops* has been discussed in a previous paper (Bohart, 1936:9). *Katastylops* and *Prostylops* were erected as subgenera by Pierce for his smallest and largest species respectively. In the author's opinion the species on which they are founded are not sufficiently different from typical *Stylops* to warrant separation.

KEY TO THE MALES OF THE GENUS STYLOPS IN NORTH AMERICA

1. Metathoracic scutellum reaching almost to the prescutum..........................2
   Metathoracic scutellum not reaching almost to the prescutum.....................5
2. Apical margin of aedeagus about half as long as the main axis...................3
   Apical margin of aedeagus less than half as long as main axis....................4
3. Postlumbium roughly semicircular, scutellum stout, not depressed nor pedunculate apically; fourth antennal segment less than twice as long as fifth....*cuneiformis*
   Postlumbium elongate, roughly oval; scutellum slender, apically depressed; fourth antennal segment more than twice as long as fifth.................*leechi*
4. Species stout; postscutellum, posterior to the postlumbium, about as long as broad ....*timberlakei*
   Species slender; postscutellum, posterior to the postlumbium, much longer than broad ....*pacifica*
5. Prescutum flat, with square posterior angles...................................6
   Prescutum convex 7

6. Last antennal segment slightly shorter than fourth......................*shannoni*
   Last antennal segment longer than fourth; apical margin of aedeagus two-
   thirds the length of the main axis, apical process long, slender, and tapering
   ....*vandykei*
7. Fourth antennal segment about twice as long as fifth...........................8
   Fourth antennal segment less than twice as long as fifth.........................9
8. Last antennal segment almost twice (19:10) as long as the fifth..............*elongata*
   Last antennal segment about one and a third (19:15) times as long as the
   fifth ....*medionitans*
9. Apical margin of aedeagus two-thirds the length of main axis, apical process
   long, slender, and tapering..*crawfordi*
10. Sixth antennal segment longer than the fourth, which is inserted about half its
    length from the base of the third segment.............................*duboisi*
    Sixth antennal segment slightly shorter than the fourth, which is inserted less
    than a third its length from the base of the third segment..............*salicifloris*

Stylops salicifloris Pierce
(Fig. D, 11–12)

Stylops salicifloris Pierce, 1909:106, 1918:453 (holotype, USNM).
Stylops centroclarus Bohart, 1937a:50 (holotype, CAS).

This is one of the commonest species of Strepsiptera, particularly in the West where it occurs on several *Trachandrena*. The interspiracular area of the female is very light and, after slight clearing in KOH, becomes transparent in strong contrast to the surrounding areas of the cephalothorax. The basal band is almost invariably convex along its anterior margin. The mandibles are usually bluntly pointed and with a more or less distinct basal tubercle (weak in type). The spiracles are usually prominent laterally. Characteristic of the species is the darkened area in the form of one or two spots along the anterior margin of the spiracular area.

There is a possibility that *salicifloris* is synonymous with *hippotes* Pierce. The type of the latter species from Ohio and one specimen in the author's collection from Illinois do not have the darkened region along the anterior margin of the spiracular area, and the anterior margin of the basal band is wavy. Otherwise they check closely with *salicifloris*.

Hosts.—*Andrena* (*Trachandrena*) *salicifloris* Ckll., *quintiliformis* Vier., n. sp. near *marioides* Vier., *cleodora* Vier., *hippotes* Robt.; E. G. Linsley determinations.
Distribution.—Pacific Coast.

Stylops nudae Pierce
(Fig. E, 31–32)

Stylops nudae Pierce, 1911a:495, 1918:452 (holotype, USNM).

Although very close to the preceding species, *nudae* differs in the female by the absence of a darkened region along the anterior margin of the spiracular area and by its more slender mandibles.

Host.—*Andrena* (*Trachandrena*) *nuda* Robt., Carlinville, Ill.

Stylops claytoniae Pierce
(Fig. E, 29–30)

Stylops claytoniae Pierce, 1909:99, 1911a:494, 1918:448 (holotype, USNM).
Stylops imitatrix Pierce, 1909:104, 1911a:494, 1918:448 (holotype, USNM).
Stylops vierecki Pierce, 1909:110, 1911a:494, 1918:448 (holotype, USNM).

Unlike other parasites of *Trachandrena, claytoniae* has no clear, well defined spiracular area, although this part is sometimes light-colored. Characteristic of the species are the convex anterior margin of the basal band and the prominent basal tubercle of the mandibles. The latter are also strongly rounded, bluntly pointed, and thick-rimmed.

Hosts.—Andrena (Trachandrena) imitatrix Cr., *claytoniae* Robt.
Distribution.—Georgia; Texas; new records, Oklahoma, Illinois.

Stylops shannoni (Pierce)

Neostylops shannoni Pierce, 1918:457 (holotype, USNM).
Stylops shannoni, Bohart, 1936:10.

This species is known only from a single specimen caught in flight. It is probable that *shannoni* represents the male of *erigeniae;* the types of both were collected on Plummer's Island, Maryland near the end of March.

The large flat prescutum is distinctive. The thoracic structure is very similar to that of *vandykei*. The antennae are normally flattened, not barrel-like as figured in Pierce, and the last antennal segment is only slightly shorter than the fourth. The postscutellum is shorter than in *vandykei*.

Stylops vandykei Bohart
(Fig. D, 23–24)

Stylops vandykei Bohart, 1936:11, 1937a:49 (holotype, CAS).

Its host is one of the largest *Andrena*, and *vandykei* is among the largest of the *Stylops*. The size of the female is greater than in any other described species, exceptional individuals measuring almost two millimeters across the spiracles. The female has a very narrow basal band which is straight along the anterior margin. In this respect it resembles *crawfordi*, which, however, lacks the strong basal tubercle of the mandible characteristic of *vandykei*. The large, flat prescutum, long last antennal segment, and peculiar aedeagus of the male separate it readily. A pair was taken in copulation by the author in March, 1937.

Hosts.—Andrena perimelas Ckll. and *A. carliniformis* Ckll. on *Brassica* and *Ranunculus*.
Distribution.—San Francisco Bay region (on *perimelas*) and Klamath Lake, Oregon (on *carliniformis*).

Stylops crawfordi Pierce
(Fig. D, 33–34)

Stylops crawfordi Pierce, 1909:100 (holotype, USNM).
Neostylops crawfordi Pierce, 1918:456.
Stylops crawfordi Bohart, 1936:11.

The aedeagus of male *crawfordi* is similar to that of *vandykei*, but the prescutum of the former is small and convex. The outstanding feature of the

female is the narrow basal band which hardly encroaches on the thorax. The premandibular area is small, and in a series of topotype specimens examined the mandibles were without a basal tubercle.

Host.—Andrena crawfordi Vier., Dallas, Texas.

Stylops medionitans Pierce
(Fig. E, 3–4)

Stylops medionitans Pierce, 1918:450.
Stylops medionitans, Bohart, 1936:12, 1937a:50.

S. medionitans is a common species throughout California, parasitizing various species of the *A. medionitens* group. The male can be recognized by the characters given in the key. The female has a short, broad head, no premandibular area, slightly concave anterior margin of the basal band, and mandibles without a basal tubercle.

Hosts.—Andrena medionitens Ckll., *scurra* Vier., and three other species near *medionitens.*
*Distribution.—*Colorado (type locality) ; California ; Oregon.

Stylops heterocingulata Bohart
(Fig. E, 25–26)

Stylops heterocingulatus Bohart, 1937a:55 (holotype, CAS).

Known only from the female, this species is characterized by its peculiar basal band, which is narrow, slightly convex along its anterior margin, and darker on the cephalothorax than on the abdomen. The mandibles are very thick-rimmed and without a basal tubercle.

Hosts.—Andrena pensilis Timb., *angustitarsata huardi* Vier. (E. G. Linsley det.), *opaciventris* Ckll.
*Distribution.—*California: Sacramento and San Joaquin valleys, San Francisco Bay region; Oregon: Corvallis, The Dalles.

FIG. D

Cephalothoraces and mandibles of female *Stylops* (camera lucida drawings)

1–2. *Stylops pacifica* Bohart, metatype.
3–4. *Stylops oklahomae* Pierce, holotype.
5–6. *Stylops grandior* Pierce, holotype.
7–8. *Stylops bruneri* Pierce, holotype.
9–10. *Stylops timberlakei* Bohart, paratype.
11–12. *Stylops salicifloris* Pierce, holotype.
13–14. *Stylops subcandidae* Pierce, holotype.
15–16. *Stylops polemonii* Pierce, holotype.
17–18. *Stylops duboisi* Bohart, paratype.
19–20. *Stylops californica* Pierce, holotype.
21–22. *Stylops solidulae* (Pierce), holotype.
23–24. *Stylops vandykei* Bohart, paratype.
25–26. *Stylops apicalis* Bohart, metatype.
27–28. *Stylops cornii* Pierce, holotype.
29–30. *Stylops elongata* Bohart, metatype.
31–32. *Stylops vicinae* Pierce, holotype.
33–34. *Stylops crawfordi* (Pierce), holotype.
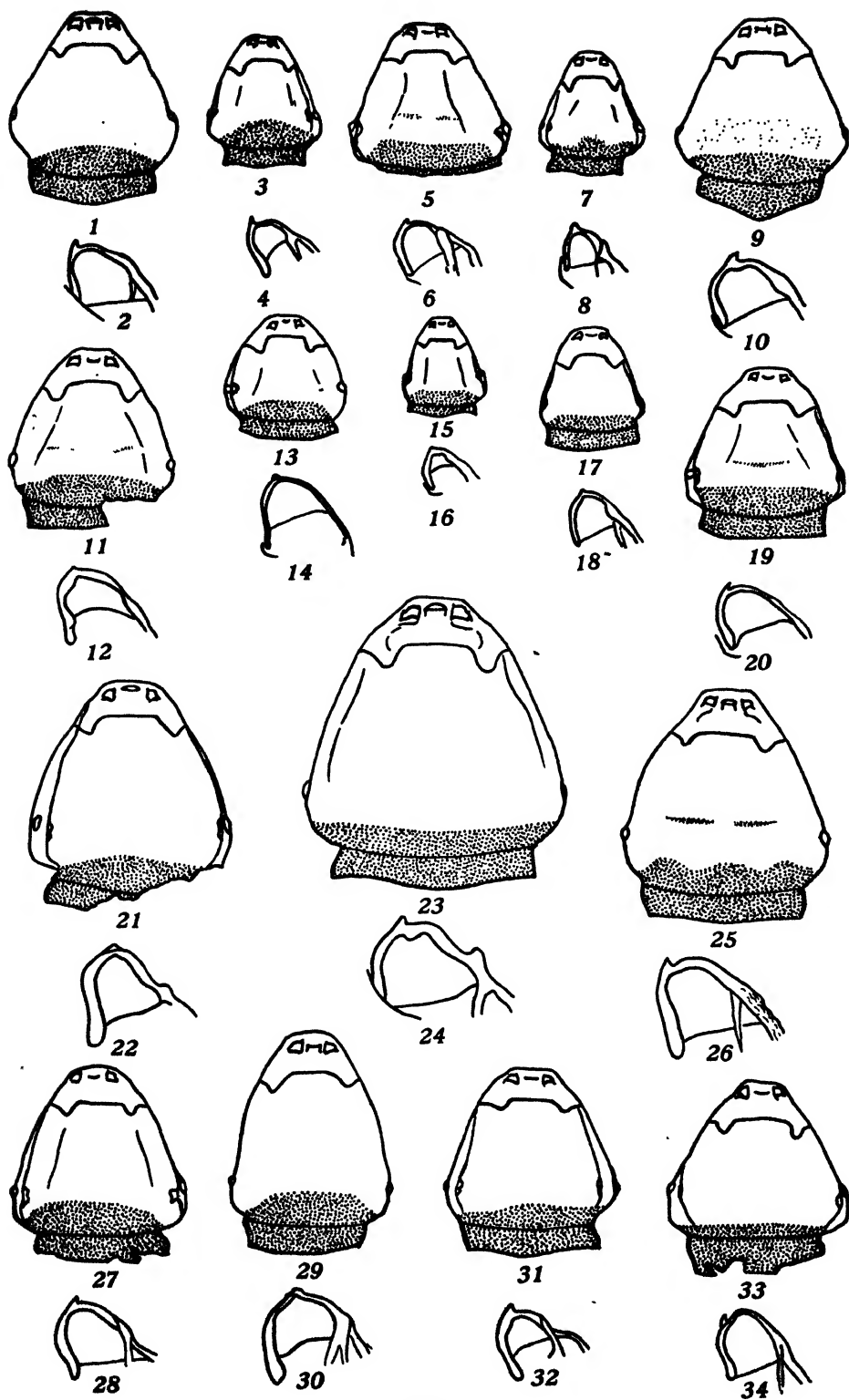
Fig. D.

Stylops pacifica Bohart
(Fig. C, 22; fig. D, 1–2; fig. F, 1)

Stylops pacificus Bohart, 1936:15, 1937a:50 (holotype, CAS).

This is probably the most abundant species of *Stylops* in northern California. The author has examined several hundred specimens including a number of males. The latter are slender insects with very large wings. The metathoracic scutellum is slender and reaches almost to the small prescutum. The basal band of the female is strongly convex, and the cephalothorax is usually spade-shaped. The first larva is peculiar in having stylets only one-fifth as long as the rest of the body whereas in most other species they are one-third or more.

Hosts.—*Andrena (Pterandrena) complexa* Vier., *suavis* Timb., on *Ranunculus.*
Distribution.—Northern California; Oregon.

Stylops timberlakei Bohart
(Fig. D, 9–10)

Stylops timberlakei Bohart, 1936:14, 1937a:50 (holotype, CAS).

Although closely related to *pacifica,* this species can be distinguished in the male by its more robust form and the slightly longer process of the aedeagus. The female cephalothorax is narrower apically, and the outer margin of the mandibles is more sharply curved. Also the basal band is less convex along its anterior margin. However, intermediate specimens are very difficult to separate.

Host.—*Andrena macrocephala* Ckll., on *Nemophila,* Riverside, California, March.

Stylops leechi Bohart, n. sp.
(Fig. C, 13, 14; fig. F, 2, 3, 6)

Related to *timberlakei* and *pacifica, leechi* can be separated in the male by its differently shaped aedeagus, the apical margin of which is about half the length of the main axis. Furthermore, it is a larger species than either of the

FIG. E

Cephalothoraces and mandibles of female *Stylops* (camera lucida drawings)

1–2. *Stylops bipunctatae* Pierce, holotype.
3–4. *Stylops medionitans* Pierce, holotype.
5–6. *Stylops sparsipilosae* Pierce, holotype.
7–8. *Stylops erigeniae* Pierce, holotype.
9–10. *Stylops swenki* Pierce, cotype.
11–12. *Stylops advarians* Pierce, holotype.
13–14. *Stylops moestae* Pierce, holotype.
15–16. *Stylops bisalicidis* Pierce, holotype.
17–18. *Stylops multiplicatae* Pierce, holotype.
19–20. *Stylops nubeoulae* Pierce, holotype.
21–22. *Stylops mandibularis* Pierce, holotype.
23–24. *Stylops oressoni* Pierce, holotype.
25–26. *Stylops heterocingulata* Bohart, paratype.
27–28. *Stylops hippotes* Pierce, holotype.
29–30. *Stylops claytoniae* Pierce, holotype.
31–32. *Stylops nudae* Pierce, holotype.
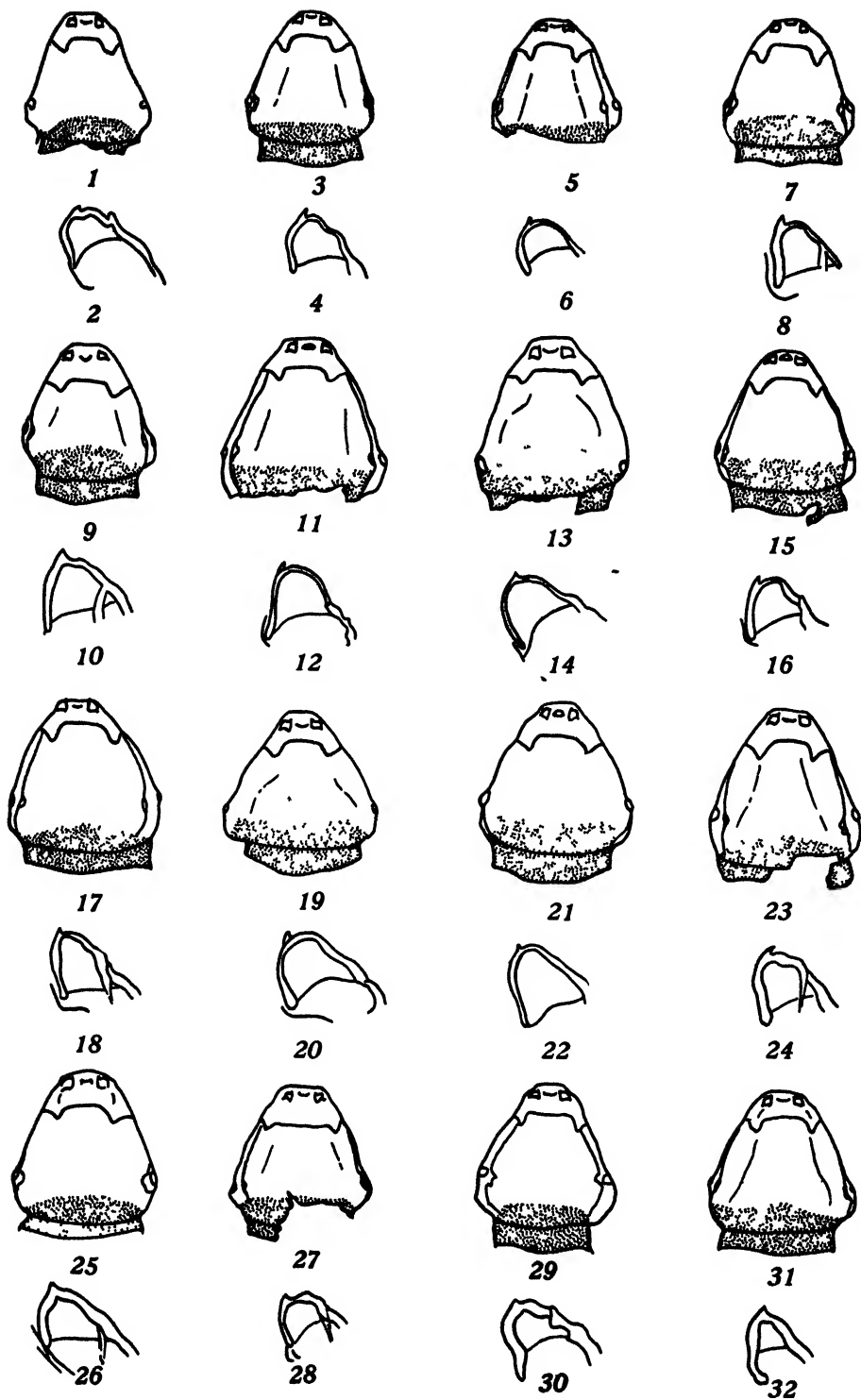
Fig. E.

other two. The scutellum is strongly pedunculate anteriorly, distinguishing the species from *cuneiformis*. The female is quite distinct from all other described species by virtue of the broad, darkly pigmented area in front of the basal band. In this respect it differs decidedly from *advarians* Pierce, which is presumably also parasitic on *A. advarians* Vier.

Description.—Male. Black; mandibles, tarsi, and ninth sternite yellowish. Antennal segments three to six with the length ratio 49:23:11:19. Segments of palpus subequal in length, terminal segment slightly longer than fourth antennal segment. Metaprescutum flat, sharply truncate behind, almost as long as scutellum at middle; scutellum pedunculate anteriorly, almost reaching prescutum; postlumbium longer than broad, longer than scutellum at middle; postscutellum very long, deeply emarginate anteriorly; posterior coxa about three times as long as width at apex, more than half (7:12) as long as the hind femur. Aedeagus slender, apical margin strongly curved and about half the length of main axis, inner margin weakly convex, not sharply emarginate before the process, which is at right angles to main axis. Length of body excluding antennae, 3.0 mm.; length of antennae, 0.8 mm.; width of head, 0.82 mm.; wing expanse, 6.5 mm.

Female. Cephalothorax testaceous on the anterior half; a broad transverse area in front of spiracles fusco-testaceous, marked with two pale spots; basal band fuscous. Cephalothorax about as broad as long, apical margin convex, lateral margins slightly convex from spiracles to mandibles; mouth broadly oval; mandible with a large, sharp, apical tooth, strongly rounded outer apical angle, and thin marginal rim; spiracles hardly exceeding the lateral margins. Basal band broad, more than half on the thorax, anterior margin convex. Width of cephalothorax at spiracles, 1.16 mm.; width at base of mandibles, 0.44 mm.; width at base of head, 0.69 mm.; width at base of cephalothorax, 0.89 mm.; length from front edge of spiracles to apex, 0.83 mm.; length of cephalothorax, 1.16 mm.

Holotype, male, March 14, 1933. Allotype, female, March 13, 1933. Paratypes, one male, February 29, 1932, in flight, J. D. Gregson, collector; ten females, March 14–21, 1933. All type material was collected at Vancouver, B.C., by H. B. Leech except as noted. Holotype to be deposited in the Canadian National Collection, other type material in the California Academy of Sciences and in the collection of the author.

Host.—*Andrena advarians* Vier. (E. G. Linsley det.)

Stylops cuneiformis Bohart

Stylops cuneiformis Bohart, 1936:16 (holotype, CAS).

The nondepressed, wedge-shaped scutellum is characteristic of the species. The scutum is almost completely divided. The fourth antennal segment is twice as long as the fifth and longer than the sixth. The apical process of the aedeagus is very slender and is about two-thirds the length of the main axis. Only the male is known, taken from a puparium in *Andrena* species at Coronado, California.

Stylops swenki Pierce
(Fig. E, 9–10)

Stylops swenki Pierce, 1909:108, 1918:447 (holotype, USNM).
Stylops asteridis Pierce, 1911a:494, 1918:443 (holotype, USNM).

The retouched photomicrograph by Pierce (1909) does not adequately illustrate this species. The holotype is angled in the balsam mount in such a way as to be difficult to study. Two specimens in the author's collection extracted from an *Andrena* determined by M. Swenk as *solidaginis* Robt. check closely

with a paratype of *swenki* and the holotype of *asteridis* at the United States National Museum. Additional specimens of *asteridis* borrowed from the Museum of Comparative Zoölogy have also been examined.

The basal band is characteristically convex along its anterior margin. Although not sharply delimited, the spiracular area is much lighter than surrounding areas. The mandibles are placed well back on the head leaving a distinct premandibular area. The mandibles are thick-rimmed, without a basal tubercle, but with strongly undulate outer margins. The terminal stylets of the first larva are less than half the length of the rest of the body.

Hosts.—Andrena (Pterandrena) species near *lincolnella* Ckll., E. G. Linsley det. (=*A. solidaginis* of Pierce) ; *asteris* Robt.

*Distribution.—*Nebraska, Illinois, Pennsylvania.

Stylops mandibularis Pierce
(Fig. E, 21–22)

Stylops mandibularis Pierce, 1911a:494, 1918:444 (holotype, USNM).
Stylops sinuatus Pierce, 1918:450 (holotype, USNM).

In addition to the type material two females of *mandibularis* have been studied from the Museum of Comparative Zoölogy. There is little doubt that *sinuatus* is a variant of the same species.

The large, smoothly rounded mandibles without basal tubercle are distinctive. A definite premandibular area is present ; lateral margins of the cephalothorax are often sinuate ; and the broad, basal band is straight or somewhat irregular along its anterior margin.

Host.—Andrena mandibularis Robt., Carlinville, Illinois.

Stylops bipunctatae Pierce
(Fig. E, 1–2)

Stylops bipunctatae Pierce, 1909:98, 1918:443 (holotype, USNM).

The exceptionally prominent basal tubercle is outstanding in the type specimens. The basal band is convex at its anterior margin, and the spiracles do not exceed the margins of the cephalothorax.

Host.—Andrena bipunctata Cr.
*Distribution.—*Indiana, Nebraska, Wisconsin.

Stylops bisalicidis Pierce
(Fig. E, 15–16)

Stylops bisalicidis Pierce, 1918:446 (holotype, USNM).
Stylops diabola Pierce, 1918:454 (holotype, USNM).

The holotype female of *bisalicidis* is practically identical with that of *diabola*. The basal band is broad and with a straight anterior margin. The thinrimmed mandibles are placed so as to leave no premandibular area, and no basal tubercle is present. The outer margin is undulate, however, and calloused at the base.

Host.—Andrena bisalicis Vier.
*Distribution.—*Alabama, North Dakota.

Stylops elongata Bohart
(Fig. D, 29–30)

Stylops elongatus Bohart, 1937a:53 (holotype, CAS).

The fifth antennal segment of the male is not more than half as long as either the fourth or sixth segments. In this respect it differs from all other described species with a broad scutal bridge. The female has the spiracles placed far back on the cephalothorax, being rivaled in this character only by *moestae* Pierce. The basal band is convex; the mandibles are weakly toothed at the apex; the premandibular area is prominent; and the cephalothorax is considerably longer than broad.

Hosts.—Andrena oenotherae Timb. and *blaisdelli* Ckll.
Distribution.—Southern California.

Stylops bruneri Pierce
(Fig. D, 7–8)

Stylops bruneri Pierce, 1909:98, (holotype, USNM).
Stylops hartfordensis Pierce, 1909:103, 1911a:494, 1918:454 (holotype, USNM).
Stylops nasoni Pierce, 1909:104, 1918:447 (holotype, USNM).
Stylops andrenoides Pierce, 1911a:493, 1918:450 (holotype, USNM).
Stylops salictariae Pierce, 1918:449 (holotype, USNM).

It is perhaps remarkable that this species is parasitic on four different species of bees belonging to three different subgenera, *Andrena, Parandrena,* and *Platandrena.* This situation would not be at all unusual if parasites of Homoptera were concerned, but *Stylops* are as a rule more host specific. Apparently certain species, if given the opportunity, are able to adjust themselves to several hosts. In this instance all four species of bees become infested with *bruneri* triungulins when visiting the flowers of willow.

The basal band of the female has a distinctively wavy anterior margin. It is depressed on either side of the middle where it gradually fuses forward a short way into the cephalothorax. The mandibles have a weakly defined apical tooth and a large subbasal tubercle, which hardly surpasses the lateral edge of the mandible. These two features separate it from all other described species. Also the cephalothorax is often longer than broad, and the premandibular area is practically nonexistent.

Hosts.—Andrena salictaria Robt., *illinoiensis* Robt., A. *(Platandrena) nasoni* Robt., A. *(Parandrena) andrenoides* Cress.
Distribution.—Nebraska, Illinois, Pennsylvania, Georgia; new record, Colorado.

Stylops vicinae Pierce
(Fig. D, 31–32)

Stylops vicinae Pierce, 1909:110, 1918:453 (holotype, USNM).

The four female specimens of this species seen by the author possess the following specific characters: Premandibular area small, mandibles with a distinct basal tubercle, spiracles prominent laterally, and anterior margin of basal band irregularly convex. The species is larger than the average, the

type specimen measuring 1.13 mm. at the spiracles. Stylets of the first larva are about two-thirds the length of the rest of the body.

Host.—*Andrena vicina* Smith.
Distribution.—Eastern Canada, New Hampshire, Massachusetts, Maryland.

Stylops cornii Pierce
(Fig. D, 27–28)

Stylops cornii Pierce, 1909:100, 1918:452 (holotype, USNM).
Stylops graenicheri Pierce, 1909:103, 1918:453 (holotype, USNM).

S. cornii is a large species with a slightly convex anterior margin of the basal band. The premandibular area is obsolete, and the mandibles have a slight tubercle or swelling at the middle of the outer margin. The spiracles exceed the margins of the cephalothorax.

Hosts.—*Andrena commoda* Sm., *nivalis* Sm.; Milwaukee, Wisconsin.

Stylops apicalis Bohart
(Fig. D, 25–26)

Stylops apicalis Bohart, 1937a:54 (holotype, CAS).

This is one of the most characteristic species of *Stylops*. The combination of the narrow apex, prominent mandibular area; two dark spots in front of the spiracular area, and wavy anterior margin of the basal band make it a very distinct species. Although numerous females have been studied by the author, no males have been seen.

Host.—*Andrena saccata* Vier.
Distribution.—California: Carmel, San Francisco Bay region. Oregon: Blue Mountains.

Species of *Stylops* of Uncertain Position

Stylops advarians Pierce, 1909:97, 1918:455 (holotype, USNM).
Stylops californica Pierce, 1909:98, 1918:452 (holotype, USNM).
Stylops childreni Gray, 1832:684; Pierce, 1909:96.
Stylops cressoni Pierce, 1909:102, 1918:453 (holotype, USNM).
Stylops grandior Pierce, 1918:451 (holotype, USNM).
Stylops hippotes Pierce, 1909:103, 1918:447 (holotype, USNM).
Stylops moestae Pierce, 1918:443 (holotype, USNM).
Stylops multiplicatae Pierce, 1909:104, 1918:445 (holotype, USNM).
Stylops neonanae Pierce, 1918:454 (holotype, ANSP).
Stylops nubeculae Pierce, 1909:105, 1918:444 (holotype, USNM).
Stylops oklahomae Pierce, 1909:110, 1918:449 (holotype, USNM).
Stylops packardi Pierce, 1909:105.
Stylops solidulae Pierce, 1909:107, 1918:457 (holotype, USNM).
Stylops sparsipilosae Pierce, 1909:108, 1918:446 (holotype, USNM).
Stylops subcandidae Pierce, 1909:108, 1918:444 (holotype, USNM).

Nomen Nudum

Stylops dunningi Pierce, 1918:438.

Pseudostylops Bohart, n. gen.
(Genotype *Pseudostylops desertorum* Bohart)

The bee genus *Halictoides* has previously been recorded as stylopized by Friese from Innsbruck, Austria. Until European specimens are examined, it will not be certain that they fall under *Pseudostylops*, although this seems likely, judging from the occurrence of *Stylops*, *Crawfordia*, and *Halictoxenos* on both continents.

Pseudostylops seems most closely related to *Stylops*, but the cephalothorax is shaped more as in *Hylecthrus*. The width at the base of the mandibles is three-fifths, and the width at the base of the head is four-fifths, the breadth at the spiracles, as compared with two-fifths and three-fifths respectively in *Stylops*. The mandibles and basal band are similar to those of *Stylops*, but the former are much farther apart, and the portion of the basal band on the thorax is lighter. The presence of five genital tubes differentiates the genus from *Crawfordia* or *Hylecthrus*.

The first larvae are very bristly, and the arrangement of the various bristles is characteristic. Of particular interest is the double row of small bristles on the abdominal tergites in addition to the usual terminal row.

Description.—Male. Unknown.

Female. Cephalothorax three-fifths as broad at the base of the mandibles and four-fifths as broad at the base of the head as at the spiracles; basal band transverse, largely on abdomen; mandibles situated about three mandible widths apart, pointing inward at about a forty-five degree angle; head distinguishable at the base almost to the lateral margins. Abdomen with five genital openings on sternites two to six inclusive; with a single pair of tracheal tubes running posteriorly.

First larva. Compound eye with five ocelli, three dorsal, one lateral, and one ventral; only a single dorsal bristle evident near the middle ocellus; head broader than long. Front and middle tarsi long pulvilliform, hind tarsus long setiform. Coxae three-bristled, femora one-bristled; four to six long bristles between each pair of coxae. Second to ninth tergites each with about twenty short and ten long bristles arranged regularly along their posterior margins; ninth tergite laterally with a long, stout bristle which is about one-quarter to one-fifth as long as the single pair of terminal stylets; the other tergites each with a slender lateral bristle.

Pseudostylops desertorum Bohart, n. sp.
(Fig. C, 17, 18, 23, 24)

Description.—Female. Cephalothorax almost square, head and spiracular areas light, remainder of thorax testaceous, basal band fusco-testaceous. Apex of head very broad, slightly convex; mandibles approximately triangular, with a single, large apical tooth; base of head about half the distance between spiracles and apical angle. Spiracles large, hardly exceeding the margins. Middle length of basal band about one-sixth its breadth. Width of cephalothorax at spiracles, 0.55 mm.; width at base of mandibles, 0.35 mm.; width at base of head, 0.43 mm.; width at base of cephalothorax, 0.46 mm.; length from front edge of spiracles to apex, 0.33 mm.; length of cephalothorax, 0.46 mm.

Holotype, female, and five paratype females, Indio, California, March 25, 1937, G. E. and R. M. Bohart, collectors. Holotype to be deposited in the California Academy of Sciences, other type material in the author's collection.

Host.—*Halictoides boregoensis* Michener (G. E. Bohart det.).

Genus *Halictoxenos* Pierce
(Genotype *Halictoxenos jonesi* Pierce)

Halictoxenos Pierce, 1908:82, 1909:147, 1911*b*:20, 1918:458.
Apractelytra Pierce, 1908:79, 1909:151, 1911*b*:22, 1918:458.
Halictostylops Pierce, 1909: 21, 1911*b*:112, 1918:459.
Halictophilus Pierce, 1909:151, 1911*b*:21, 1918:458.
Augochlorophilus Pierce, 1911*b*:22, 1918:489.
Halictoxenus Perkins, 1918:75.
Halicostylops Noskiewicz and Poluszyński, 1924*a*:869.
Halictoxenos, Noskiewicz and Poluszyński, 1924*b*:182.
Halictoxenos, Ulrich, 1930*b*:17.

The paucity of males of the genus *Halictoxenos* has always presented a perplexing problem to workers on Strepsiptera. Only a few male specimens are on record as compared with hundreds of females. It is to this genus that parthenogenesis and polyembryony have been ascribed. An explanation that apparently fits the facts is that the male parasites emerge and copulate with the females in the fall, but only the latter overwinter with the adult *Halictus* and can thus be collected in the spring. All the males recorded have been captured in the late summer or fall.

Description.—Male. Antennae four-segmented, the third and fourth subequal in length. Scutal bridge broad (not as figured in Pierce, 1909) ; scutellum truncate anteriorly, smaller than the postlumbium ; radius, media, cubitus, two vannal veins, and one jugal vein present in the hind wing ; two detached pieces between the radius and media ; hind legs exceptionally stout, much more so than in *Stylops*. Aedeagus with a long, curved, basal shaft and a short, stout, apical process at right angles to the main axis.

Female. Head not separated from the thorax ventrally by lateral extensions of the brood-canal opening as in *Stylops* and *Pseudostylops;* mandibles deformed, often apically cleft. Usually with a group of enlarged transparent cells or "pori" in or in front of the spiracular area (scolopophorous organs?). Abdomen with five genital openings on sternites two to six inclusive.

First larva. Body densely bristled, especially on the posterior margins of the abdominal segments. Compound eyes with five ocelli, only two or three of which are visible except in lateral view. Front and middle tarsi long pulvilliform, hind tarsus long setiform. Lateral bristles of the ninth tergite heavier than those of the preceding tergites ; only one pair of terminal stylets.

The synonymy in this genus was decided upon after a comparison of a long series of specimens in the author's collection with type material at the United States National Museum. The range of variation in the shape of the mandibles within a series of specimens from one locality and host indicate that this character is of doubtful value in this genus. Pierce's species were for the most part based on individual variations and the assumption of host specificity. Material borrowed from the Museum of Comparative Zoölogy from several of the hosts of Pierce's species bear out this conclusion. In all probability, *crawfordi* is the female of *jonesi,* but positive evidence is lacking. Furthermore, *nymphaeri* may be only an odd variation of *crawfordi,* although this does not seem likely.

KEY TO THE FEMALES OF HALICTOXENOS IN NORTH AMERICA

1. Cephalothorax spade-shaped, width at base of mandibles about one-third the
   width at spiracles..*nymphaeri*
   Cephalothorax almost triangular, width at base of mandibles about one-fourth
   the width at spiracles..2
2. Cephalothorax about as long as broad, basal band usually extending up to the
   prominent "pori"...*crawfordi*
   Cephalothorax considerably broader than long, basal band with anterior margin
   shaped like a broad inverted V, "pori" very indistinct or absent............*viridulae*

Halictoxenos jonesi Pierce

Halictoxenos jonesi Pierce, 1908:82, 1909:149 (holotype, USNM).

The form of the scutum and scutellum are incorrectly figured by Pierce
(1909, pl. 13, fig. 1). The scutum is broadly connected between the scutellum
and prescutum. The hind tarsi are short and stout, the first segment being
almost quadrate. The female is unknown.

Host.—*Halictus (Chloralictus)* species.
Distribution.—Texas, Louisiana.

Halictoxenos schwarzi (Pierce)
(Fig. F, 7, 8, 9, 13)

Apractelytra schwarzi Pierce, 1908:83, 1909:152 (holotype, USNM).

The figures of Pierce (1909, pl. 10, figs. 3–6) give an erroneous impression
of this species, which is a typical *Halictoxenos*. The peculiar appearance of

FIG. F

1. *Stylops pacifica* Bohart, male.
2. *Stylops leechi* Bohart, male antenna.
3. *S. leechi*, male aedeagus.
4. *Pseudoxenos lugubris* (Pierce), male antenna.
5. *P. lugubris*, aedeagus.
6. *S. leechi*, male metathorax, dorsal.
7. *Halictoxenos schwarzi* (Pierce), hind leg.
8. *H. schwarzi*, front leg.
9. *H. schwarzi*, male metathorax, dorsal.
10. *Pseudoxenos smithii* (von Heyden), male head, dorsal.
11. *P. lugubris*, male head, ventral.
12. *P. lugubris*, male metathorax, dorsal.
13. *H. schwarzi*, aedeagus.
14. *Pseudoxenos arvensidis* Pierce, aedeagus.
15. *Pseudoxenos tigridis* Pierce, aedeagus.
16. *P. lugubris*, anterior portion of hind wing.
17. *Xenos pallidus* Brues, anterior portion of hind wing.
18. *P. smithii*, aedeagus.
19. *Pseudoxenos luctuosae* (Pierce), aedeagus.
20. *P. lugubris*, front tibia and tarsus.
21. *P. arvensidis*, front tibia and tarsus.
22. *Callipharixenos muiri* Pierce, female cephalothorax, ventral.
23. *C. muiri*, head of first larva, lateral.
24. *P. lugubris*, adult female.
25. *Xenos peckii* Kirby, adult female.
26. *P. lugubris*, posterior end of first larva, ventral.
27. *X. pallidus*, adult female.
28. *X. pallidus*, first larva, dorsal.
29. *X. pallidus*, first larva, ventral.
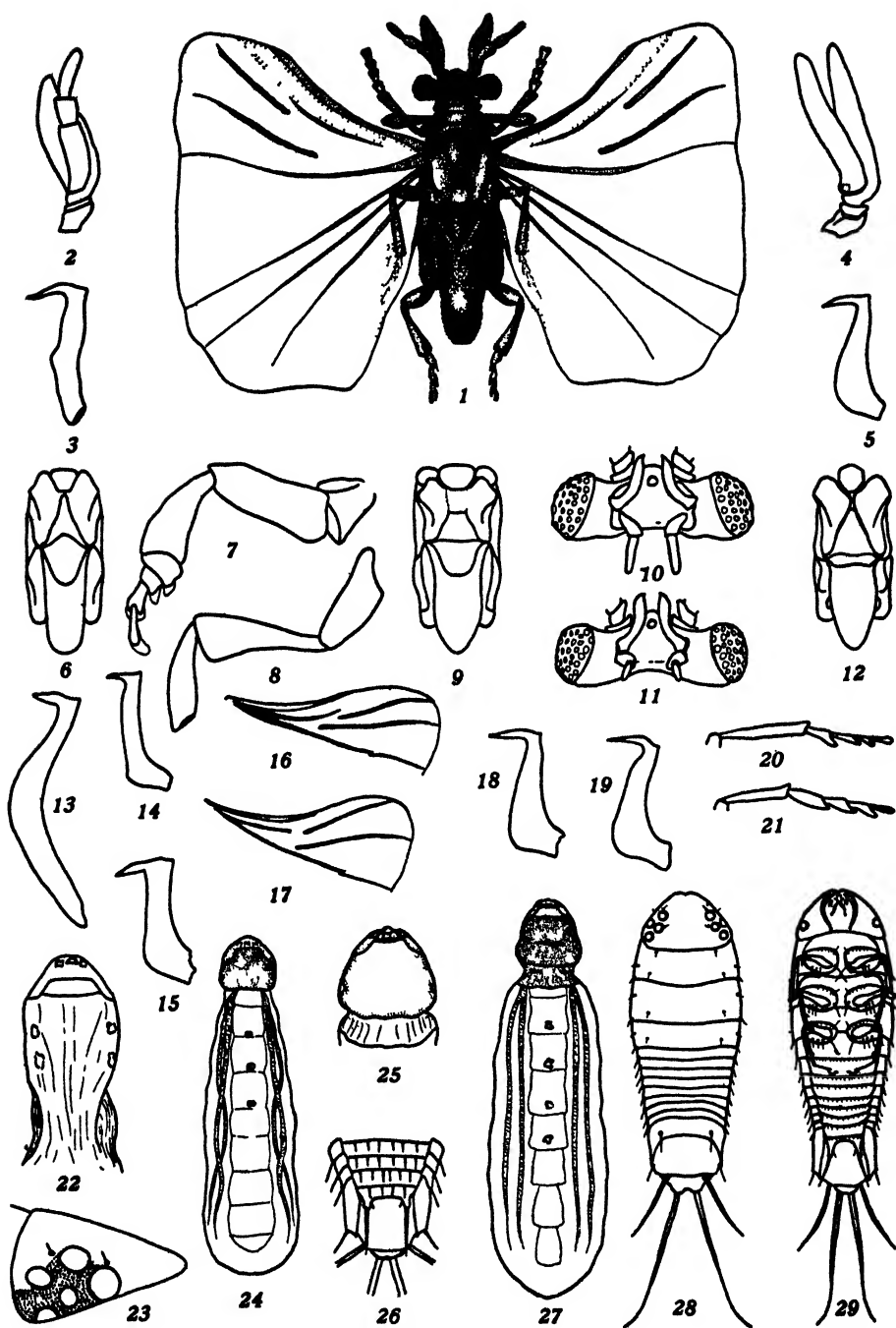
Fig. F.

the postscutellum in his drawing is the result of his representation of wrinkles in the dried specimen. Actually the metathorax is exceedingly close to that of *jonesi.* His drawings of the maxilla and mandible are approximately correct, but the wing lacks the first detached vein shown in his drawing. Furthermore, the aedeagus is not rounded apically but hooked as in *Stylops.* Although there is a possibility that this species is synonymous with *jonesi,* the shorter post-lumbium and more slender hind legs appear sufficient to separate the two. Unfortunately the specimens of *jonesi* are not in good condition for study, and accurate comparisons could not be made. The host of *schwarzi* was un-known to Pierce, but the subsequent capture by J. C. Bridwell of a male in a *Halictus* has cleared up this point.

Host.—Halictus (Chloralictus) geminus Sandhouse (G. Sandhouse det.), Clifton, Va., Sept. 4, 1933, J. C. Bridwell, collector. Holotype locality, Washington, D. C.

Halictoxenos crawfordi Pierce
(Fig. C, 11, 12, 21)

Halictoxenos crawfordi Pierce, 1909:148 (holotype, USNM).
Halictoxenos graenicheri Pierce, 1909:148 (holotype, USNM).
Halictoxenos sephyri Pierce, 1909:148 (holotype, USNM).
Halictoxenos versati Pierce, 1909:148 (holotype, USNM).
Halictoxenos sparsi Pierce, 1909:148 (holotype, USNM).
Halictoxenos graeinicheri Pierce, 1909: 150 (err. typ.).

Hosts.—Halictus (Chloralictus) bruneri Cwfd., *albipennis* Robt., *versatus* Robt., *zephyrus* Sm., *sparsus* Robt.; new records, *incompletus* Cwfd., *punctatoventris,* Cwfd., species near *nevadensis* Ckll.
*Distribution.—*Nebraska, Wisconsin, Oklahoma. New records: California, San Bernar-dino, Tulare, Santa Clara, Alameda counties; Illinois, Carlinville; North Carolina, Raleigh.

Halictoxenos nymphaeri Pierce

Halictoxenos nymphaeri Pierce, 1911a:496 (holotype, USNM).

Host.—Halictus (Chloralictus) nymphaerum Robt., Illinois.

Halictoxenos viridulae Pierce

Halictoxenos viridulae Pierce, 1911a:496 (holotype, USNM).

Host.—Augochlora viridula Smith, Illinois.

Genus *Crawfordia* Pierce
(Genotype *Xenos pulvinipes* Pierce)

Crawfordia Pierce, 1908:80, 1909:153, 1911b:22, 1918:459.
Xenoides Pierce, 1909:153.
Crawfordia, Ogloblin, 1924:110.
Crawfordia, Ulrich, 1930b:22.

No males of this genus have been seen by the author, but, according to Pierce's figures and descriptions (1908, 1909), it is distinguished from *Halicto-xenos* by its aedeagus and its wing venation. The aedeagus, as described by Pierce (1909:153), "quickly dilates from a slender tube into a very acute

curved process." The two detached veins between the radius and media of *Halictoxenos* are apparently absent in *Crawfordia*.

The head of the female is completely fused ventrally to the thorax, but a peculiar, rodlike thickening extends from the brood-canal opening to the region of the spiracles and ends in three groups of enlarged cells resembling the "pori" of *Halictoxenos*. The basal band is dark and prominent; the mandibles are triangular and very similar to those of *Pseudostylops;* and, according to Ulrich, the abdomen has three genital openings.

KEY TO THE FEMALES OF CRAWFORDIA IN NORTH AMERICA

Mandible at least as broad as long; anterior margin of basal band evenly convex; rodlike thickening ending about at the region of the spiracles in three short branches ....*pulvinipes*

Mandible longer than broad; anterior margin of basal band not evenly convex; rodlike thickening ending beyond the spiracles.............................*cockerelli*

Crawfordia pulvinipes Pierce
(Fig. C, 15, 16)

Xenos pulvinipes Pierce, 1904:167 (holotype, W. D. Pierce collection).
Crawfordia pulvinipes Pierce, 1908:80, 1909:153, 1911a:497.
Crawfordia labrosi Pierce, 1911a:497 (holotype, USNM).
Crawfordia rudbeckiae Pierce, 1911a:497 (holotype, USNM).

In addition to the type material of *labrosi* and *rudbeckiae* two specimens borrowed from the Museum of Comparative Zoölogy have been studied. These were parasites from *Pseudopanurgus rudbeckiae* and *P. solidaginis,* collected at Carlinville, Illinois.

Hosts.—Pseudopanurgus innuptus (Ckll.), *labrosus* Robt., *rudbeckiae* Robt., and *solidaginis* Robt.
Distribution.—Nebraska, West Point; Illinois, Carlinville.

Crawfordia cockerelli Pierce

Crawfordia cockerelli Pierce, 1909:155, 1911a:497 (holotype, USNM).
Host.—Pseudopanurgus boylei Ckll., Las Vegas, N. M., August.

Nomina Nuda

Crawfordia californica Pierce, 1918:460.
Crawfordia labrosidiformidis Pierce, 1918:460.

Genus *Hylecthrus* Saunders
(Genotype *Hylecthrus rubi* Saunders)

Hylecthrus Saunders, 1850:57, 1872:29.
Hyleohthrus Pierce, 1908:82, 1909:113, 1911b:18.
Hylecthrus, Pierce, 1918:458.
Hylecthrus, Ulrich, 1930b:16.

Our knowledge of the male of this genus is limited to the descriptions and figures of Saunders (1850, 1872). The male is characterized by its five-segmented antennae, the third segment of which is small. The wing venation does

not differ materially from that of *Halictoxenos,* and the postlumbium is moderately large.

The female was incompletely described by Saunders and the first larva was not described at all. The author has been fortunate enough to secure a long series of females and first larvae from the Sierra of California and two females from Formosa. A description based on this material follows.

Description.—Female. Cephalothorax somewhat broader than long, apex very broadly rounded. Head completely fused ventrally to the thorax, not marked off by lateral extensions from the brood-canal opening. Mandibles deformed, apically cleft, the hump surpassing the apical tooth. Premandibular area very small. Brood passage delineated by a thickened strand from each end of the brood-canal opening and running posterior to the region of the spiracles (scolopophorous organs?). Basal band obsolete. Abdomen with two genital openings.

First larva. Much less bristly than any other of the parasites on bees. Compound eye with five ocelli; two pairs of interocular bristles visible. Thoracic and first abdominal tergites with a row of small, stout bristles on either side equidistant between the middle and lateral margins; first thoracic tergite with two pairs of these bristles. Thoracic and abdominal tergites with a single lateral bristle on each side, the bristles increasing in length toward the rear. Abdominal tergites, one to eight inclusive, posteriorly margined with minute bristles; ninth tergite with a long bristle on either side of the middle. Front and middle tarsi elongate pulvilliform, hind tarsus short setiform. Abdominal sternites margined with bristles of two sizes, the longer about one-half the length of the sternites; ninth sternite with a long bristle on either side of the middle. One pair of apical stylets present.

Hylecthrus californicus Bohart, n. sp.
(Fig. C, 9, 10, 19, 20)

Description.—Male unknown.

Female. Cephalothorax slightly broader than long, testaceous. Mandible with the outer hump strongly developed, far surpassing the apical tooth; distance between the mandibles about three mandible widths. Spiracles laterally prominent. Rodlike structures in the region of the spiracles forked. Basal band obsolete. Width of cephalothorax at spiracles, 0.64 mm.; width at base of mandibles, 0.30 mm.; width at base of head, 0.45 mm.; width at base of cephalothorax, 0.53 mm.; length from front edge of spiracles to apex, 0.37 mm.; length of cephalothorax, 0.59 mm.

First larva. Length of body excluding stylets, 0.30 mm.; length of stylets, 0.13 mm.; width of head, 0.056 mm.

Holotype, female, Mammoth Lakes, Mono County, California, elevation 9000 ft., August 5, 1936, R. M. Bohart, collector. Paratypes, thirteen females, Mammoth Lakes, Mono County, California, July and August, G. E. and R. M. Bohart, collectors. Metatypes, two females, Kings River, Paradise Valley, Fresno County, California, elevation 7000 ft., July 16, 1910, E. C. Van Dyke, collector (collection of CAS).

Hosts.—*Hylaeus coloradensis* Ckll. (holotype and paratypes); *Hylaeus episcopalis* Ckll. (?) (metatypes); C. D. Michener determinations.

Genus *Xenos* Rossius
(Genotype *Xenos vesparum* Rossius)

Xenos Rossius, 1793.
Xenus authors.
Xenos, authors.
Schistosiphon Pierce, 1908:80, 1909:132.
Acroschismus Pierce, 1908:82, 1909:119.

Vespaexenos Pierce, 1909:133, 1911b:26, 1918:462.
Belonogastechthrus Pierce, 1911a:498, 1918:460 (synonym?).
Clypoxenos Brethès, 1923:45 (synonym?).

As herein redefined the genus *Xenos* includes all the Strepsiptera parasitic on the Polistinae, Vespinae, and Polybiinae. In other words it occurs only on the social wasps. *Vespaexenos* and *Belonogastechthrus* have been placed in synonymy after studies of both sexes and first larvae from *Vespa* and of the female only from *Belonogaster*. In the latter genus the females are almost identical with those from African *Polistes* also in the author's collection. Without a study of the males of *Belonogastechthrus* or *Clypoxenos* it is not absolutely certain that these are synonymous with *Xenos*.

Characteristic of the genus in the male is the wing venation, which differs only slightly but distinctively from that of *Pseudoxenos*. The radial vein is continuous or, if broken, the apical part originates on the same level as the end of the basal part and is not distinctly posterior to it as in *Pseudoxenos*. In the American *Polistes* parasites the palpus is shorter than the mandible, but in the European, *X. vesparum,* it is longer. The antennae are four-segmented and the postlumbium is short and wide as in *Pseudoxenos*. The female differs in having four, instead of three, genital tubes. This character has been definitely checked for parasites from *Mischocyttarus* in North America and *Polybia* in South America. The first larvae, like those of *Pseudoxenos*, have the ninth sternite with a pair of bristle-bearing, fleshy tubercles and the ninth tergite much larger than those preceding. It differs from *Pseudoxenos*, however, in having only very small bristles margining the sternites.

KEY TO THE SPECIES OF XENOS IN NORTH AMERICA
MALES
Underside of the body, including the head, yellow in color (best seen in dry specimens) ....*pallidus*
Underside of body, including head, light or dark brown.......................*peckii*

FEMALES
Cephalothorax longer than broad; anterior margin of darkly pigmented area forming a straight line at the base of the head.................................*pallidus*
Cephalothorax about as long as broad; anterior margin of darkly pigmented area strongly emarginate in the middle..*peckii*

Xenos peckii Kirby
(Fig. F, 25; fig. G)

Xenos peckii Kirby, 1813:100.
Xenos peckii, Brues, 1903:248.
Achroschismus wheeleri Pierce, 1908:80, 1909:129 (holotype, USNM).
Achroschismus bruesi Pierce, 1909:124 (holotype, USNM).
Achroschismus pecosensis Pierce, 1909:128 (cotypes, USNM, ANSP).
Achroschismus bowditchi Pierce, 1909:130 (holotype, USNM).
Achroschismus texani Pierce, 1909:132 (holotype, USNM).
Achroschismus maximus Pierce, 1909:132 (holotype, USNM).
Xenos auriferi Pierce, 1911a:498 (holotype, USNM).
Xenos californicus Pierce, 1918:489 (nomen nudum).
Xenos peckii authors.

As the first species of Strepsiptera described from North America, *peckii* is of more than ordinary interest. The coloration of the female cephalothorax is characteristic. The anterior, square emargination of the pigmented area contrasts with the straight margin in *pallidus*, in which species the cephalothorax is also much longer. The male is darker in color and somewhat less slender than in *pallidus*. The drawings in figure G are reproduced from a photographic copy of Peck's original unpublished drawings of the material he sent to Kirby. They are given here through the kindness of E. O. Essig, who obtained the photograph from L. P. Rockwood. The typical emargination of the pigmented area can be seen in the side view of the female cephalothorax. Long series of this species have been examined by the author from many of the subspecies of *Polistes fuscatus*. In the examination of approximately one thousand female parasites from *P. fuscatus aurifer*, it was noted that about 1 per cent of these had five genital openings on the abdomen instead of the usual four; evidently even this generic character is not invariable. In the author's opinion the several species of Pierce listed in the synonymy represent individual variants only.

Hosts.—*Polistes fuscatus* (Fabr.) and its various subspecies, *anaheimensis* Prov., *apachus* Sauss., *aurifer* Sauss., *flavus* Cr., *hunteri* Beq., *metricus* Say, *pallipes* Lepel., *variatus* Cr.
Distribution.—North America.

Xenos pallidus Brues
(Fig. F, 17, 27, 28, 29)

Xenos pallidus Brues, 1903:246.
Achroschismus hubbardi Pierce, 1908:84, 1909:122 (holotype, USNM).
Achroschismus pallidus, Pierce, 1909:126.
Achroschismus pallidus texensis Pierce, 1909:127 (holotype, USNM).

Host.—*Polistes canadensis* (Linn.) subsp. *annularis* (Linn.).
Distribution.—North America east of the Rocky Mountains.

Species of *Xenos* of Uncertain Position

Xenos nigrescens Brues, 1903:247.
Achroschismus hunteri Pierce, 1909:130 (holotype, USNM).
Achroschismus rubiginosi Pierce, 1909:132 (holotype, USNM).

Genus *Pseudoxenos* Saunders
(Genotype *Pseudoxenos schaumi* Saunders)

Pseudoxenos Saunders, 1872:44.
Paraxenos Saunders, 1872:45.
Eupathocera Pierce, 1908:79, 1909:143, 1911b:29, 1918:464.
Ophthalmochlus Pierce, 1908:79, 1909:142, 1911b:30, 1918:464.
Homilops Pierce, 1908:80, 1909:142, 1911a:503.
Leionotoxenos Pierce, 1909:137.
Monobiaphila Pierce, 1909:139, 1911b:28, 1918:463.
Sceliphronechthrus Pierce, 1909:141, 1918:468.
Tachytixenos Pierce, 1911a:501, 1911b:28.
Isodontiaphila Pierce, 1918:265.
Montezumiaphila Brethès, 1923:45 (synonym?).
Macroxenos Schultze, 1925:238.

A preliminary synonymy of *Pseudoxenos* was given in a previous paper by the author (Bohart, 1937c). The addition of *Tachytixenos, Paraxenos, Monobiaphila,* and *Isodontiaphila* should be made to the synonymy given at that time. From an examination of the genotypes at the United States National
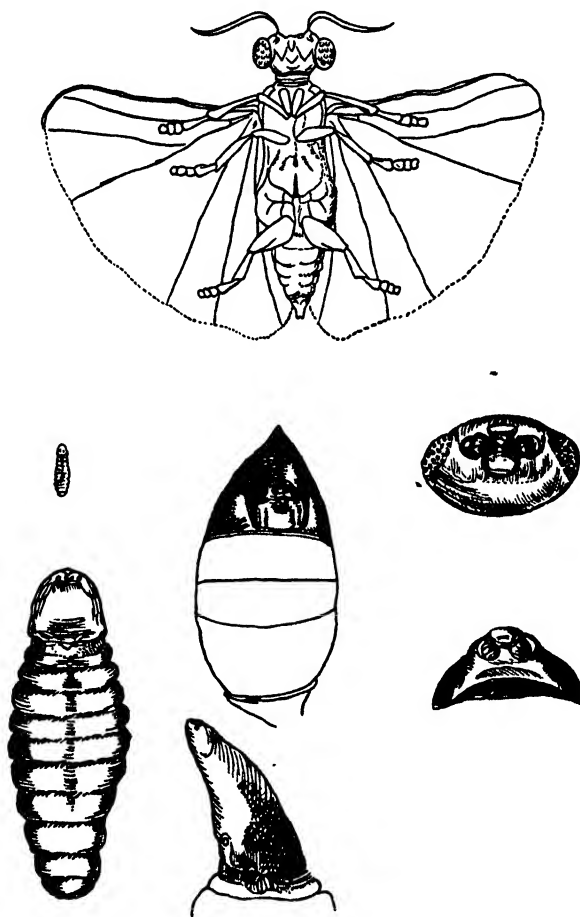
FIG. G

Xenos peckii Kirby (from a photograph of Peck's unpublished drawings of the material he sent to Kirby).

Museum and of additional material received by the author, there seems to be no doubt of their identity. *Paraxenos,* from a bembicid, is insufficiently separated by Saunders (1872). A female specimen collected by G. Bohart on *Microbembix aurata* Parker at Antioch, California is typical *Pseudoxenos.* The systematics of the genus is not in a satisfactory condition. The whole problem needs to be restudied critically with respect to host-parasite relationships.

PARTIAL KEY TO THE MALES OF PSEUDOXENOS IN NORTH AMERICA

1. Fore tarsus shorter than fore tibia..2
   Fore tarsus longer than fore tibia..4
2. Palpi as long as mandibles...*smithii*
   Palpi shorter than mandibles..3
3. Apical margin of aedeagus strongly curved outward........................*luctuosae*
   Apical margin of aedeagus only slightly curved outward....................*lugubris*
4. Aedeagus short and stout, the apical margin almost half the length of the
   aedeagus ....*tigridis*
   Aedeagus long and slender, the apical margin less than a third the length of the
   aedeagus ....*arvensidis*

Pseudoxenos smithii (von Heyden)
(Fig. F, 10, 18)

Xenos smithii von Heyden, 1867:398.
Homilops bishoppi Pierce, 1909:146 (holotype, USNM).

Hosts.—*Chlorion (Ammobia) ichneumoneum* (Linn.), *habenum* Say, *pennsylvanicum* (Linn.), *flavitarsus* (Fern.).
Distribution.—North America.

Pseudoxenos luctuosae (Pierce)
(Fig. F, 19)

Eupathocera luctuosae Pierce, 1911a:502.

Hosts.—*Podalonia violaceipennis* (Lep.) and subsp. *luctuosa* (Sm.); *P. argentifrons* (Cr.).
Distribution.—Idaho, Colorado; new records, California, Utah, Oregon, New Mexico, Arizona.

Pseudoxenos lugubris (Pierce)
(Fig. F, 4, 5, 11, 12, 16, 20, 24, 26)

Eupathocera lugubris Pierce, 1908:83, 1909:143 (holotype, Drury Collection, Cincinnati, O.).
Eupathocera pruinosae Pierce, 1909:143 (holotype, USNM).
Eupathocera pictipennidis Pierce, 1911a:502 (holotype, USNM).
Eupathocera vulgaridis Pierce, 1911a:503 (holotype, USNM).

After studying hundreds of specimens of both sexes from numerous species of *Sphex*, the author has come to the conclusion that there is only one species of *Pseudoxenos* on *Sphex* in North America. The females vary greatly in size depending upon the size of the host, but the males are much more constant.

Hosts.—*Sphex placidus* (Sm.) (=*pictipennis* Walsh), *vulgaris* (Cr.), *fragilis* (Sm.), *pruinosa* (Cr.); new records, *aberti* (Hald.), *transversus* Fern., *craspedotus* Fern., *nasalis* Prov., *breviceps* (Sm.), *aureonotatus* (Cam.), *arvensis* (Dahlb.), *urnarius* (Dahlb.).
Distribution.—North America.

Pseudoxenos tigridis Pierce
(Fig. F, 15)

Pseudoxenos tigridis Pierce, 1911a:501 (holotype, USNM).

Host.—*Odynerus (Ancistrocerus) tigris* Sauss.
Distribution.—Illinois; new records: Ontario, Ridgeway; New York, Gowanda; California, Yolo County (single parasite), Vacaville.

Pseudoxenos arvensidis Pierce

(Fig. F, 14)

Pseudoxenos arvensidis Pierce, 1911a:499 (holotype, USNM).

If it can be proved that this species is synonymous with *P. hookeri* Pierce, which occurs on a host of the same subgenus (*Rygchium verus* Cr.), that name will take precedence over *arvensidis*.

Hosts.—*Odynerus (Rygchium) arvensis* Sauss.; new record, *O. sulphureus* Sauss.
Distribution.—Illinois (on *arvensis*), California (on *sulphureus*).

Pseudoxenos louisianae (Pierce)

Leionotoxenos louisianae Pierce, 1909:138 (holotype, USNM).
Pseudoxenos histrionis Pierce, 1911a:500 (holotype, USNM).
Pseudoxenos pedestridis Pierce, 1911a:500 (holotype, USNM).

Characteristic of the species is the quadrate mandible with strongly hooked apical tooth. The portion of the thorax in the posterior emargination of the head is darkened, but the rest of the thorax, except for two indistinct lines, is light. If the mandibular character is found to be unstable, more synonymy may be necessary. For the present those species which do not agree perfectly are put in a group of uncertain position. Only when males of these are found, can their status be determined.

Species of *Pseudoxenos* of Uncertain Position

Ophthalmochlus auripedis Pierce, 1911a:503.
Monobiaphila bishoppi Pierce, 1909:139.
Ophthalmochlus duryi Pierce, 1909:142.
Pseudoxenos erynnidis Pierce, 1911a: 499.
Pseudoxenos foraminati Pierce, 1911a:499.
Pseudoxenos fundati Pierce, 1911a:500.
Leionotoxenos hookeri Pierce, 1909:139.
Leionotoxenos jonesi Pierce, 1909:138.
Pseudoxenos neomexicanus Pierce, 1918:463.
Pseudoxenos robertsoni Pierce, 1911a:501.

Family HALICTOPHAGIDAE Perkins

Halictophaginae Perkins, 1905:98.
Halictophagoidea Pierce, 1908:76, 1909, 1911b, 1918.
Halictophagidae Pierce, 1908:76, 1909, 1911b, 1918.
Dioxoceridae Pierce, 1908:76, 1909:163.
Diozoceridae Pierce, 1911a:504, 1911b, 1918.
Halictophaginae, Ulrich, 1930b:13.

The family as here constituted contains three genera distinguished by differences in the structure of the male antennae. Apparently the number of brood canals in the females is usually three but sometimes two or even one. Male halictophagids are separable from all other Strepsiptera by the combination of three-segmented tarsi and seven-segmented antennae.

Genus *Halictophagus* Curtis

Halictophagus Curtis, 1831:433.
Halictophagus, Saunders, 1872:25.
Halictophagus, Perkins, 1905:104.
Bruesia Perkins, (nec Ashmead, 1903) 1905:102.
Megalechthrus Perkins, 1905:106.
Halictophagus, Pierce, 1908:80, 1909:155, 1911*b*:39, 1918:468.
Pentacladocera Pierce, 1908:80, 1909:157, 1911*b*:36, 1918:471.
Pentoxocera Pierce, 1908:80, 1909:157.
Anthericomma Pierce, 1908:84, 1909:162.
Agalliaphagus Pierce, 1908:83, 1911*b*:37, 1918:479.
Megalechthrus, Pierce, 1909:160, 1911*b*:37, 1918:480
Neocholax Pierce, 1909:160, 1911*b*:40, 1918:480.
Pentagrammaphila Pierce, 1909:169, 1911*b*:45.
Pentosocera Pierce, 1911*a*:504, 1911*b*:38, 1918:468.
Diozocera Pierce, 1911*a*:504, 1911*b*:33, 1918:466.
Pentozoe Pierce, 1911*a*:504, 1911*b*:37, 1918:468.
Tettigoxenos Jeannel, 1913:1.
Pyrilloxenos Pierce, 1914:128.
Pyrilloxenos, Misra, 1916:124.
Tettigoxenos, Pierce, 1918:468.
Dacyrtocara Pierce, 1918:473.
Cyrtacaraxenos Pierce, 1918:475.
Indoxenos Subramanium, 1927:131.
Oedicystis Hofeneder, 1927:376.
Pseudopatella Bohart, 1937*b*:101.

The genus *Halictophagus* has been heretofore treated under the various, undefinable generic names listed above. If the criteria for genera as used in other families of Strepsiptera are applied here, it can be seen that the species under this multiplicity of names cannot be separated in the first larvae except by extremely minor differences, in the female by the number of genital tubes or in the male by other than specific characters.

The family Diozoceridae (=Dioxoceridae) of Pierce deserves special mention. It was erected by Pierce on the basis of three females and a single immature male specimen extracted from its puparium. The holotype male is mounted on its side in balsam and has lost the last three segments of the uppermost antenna. The normal seven-segmented antenna can be seen with difficulty on the other side. Pierce was misled by this circumstance and recorded the antennae as four-segmented. The true situation has been verified by other material of both sexes from the same host species borrowed from the United States National Museum.

KEY TO THE MALES OF HALICTOPHAGUS IN NORTH AMERICA AND THE WEST INDIES

1. Aedeagus rounded before the apex, not sharply angular or barbed..............*barberi*
   Aedeagus sharply angled before the apex, not rounded...........................2
2. Front femur and dorsal surface of first two antennal segments with conspicuous
      sensoria, flabellae of third and fourth antennal segments widely separated..*bidentatus*
   Front femur and dorsal surface of first two antennal segments without con-
      spicuous sensoria, flabellae of third and fourth antennal segments close together.....3

Halictophagus barberi (Pierce)
(Fig. H, 23)

Anthericomma barberi Pierce, 1908:84, 1909:162 (holotype, USNM).

Host.—Unknown.
Distribution.—Santa Fe, New Mexico.

Halictophagus mackayi (Bohart)
(Fig. H, 10, 20, 29)

Pseudopatella mackayi Bohart, 1937b: 101 (holotype, CAS).

The peculiar front tibiae of the male are unparalleled in the Strepsiptera. The mandibles of the female are slender and one-toothed.

Hosts.—*Ribautiella affinis* G. and B., *Latalus configuratus* Uhler, *Athysanella acuticauda* Baker, *Laevicephalus uhleri* Oman (P. W. Oman determinations).
Distribution.—Vonda, Saskatchewan, Canada.

Halictophagus bidentatus Bohart, n. sp.
(Fig. H, 3)

The prominent sensoria on the legs and basal antennal segments distinguish this species in the male from all others previously described. With respect to the general structure of the head proper, thorax, and aedeagus, it is similar to *mackayi*. The tibiae are strongly differentiated basally but have no projection on the front pair as in *mackayi*. The female of *bidentatus* has two distinct apical teeth on each mandible as in *oncometopiae*. However, the latter species has a proportionately shorter cephalothorax and a differently shaped pigmented area on the first abdominal sternite. Margaret MacKay of the British Museum of Natural History has kindly turned over to the author her material of this species along with an unpublished description of it.

Description.—Male. Body dark brown, hind wings and tarsi pale, second to eighth abdominal sternites with brownish spots, that of second segment divided in middle. Head wide V-shaped in dorsal aspect, tapering anteriorly. Mandibles long triangular and sharply pointed; maxillary segments subequal in length; antenna with all segments covered with sensoria, basal parts of third and fourth segments elongated widely separating their flabellae, flabellum of fourth segment enlarged and with an inner concavity within which the fifth and sixth segments fit in repose, fifth to seventh segments subequal in length but much shorter than third or fourth segments. Prothorax not sunken into head. Metaprescutum subtriangular, longer than broad; scutellum broad and five-cornered; postlumbium

nearly rectangular, twice as broad as long; postscutellum as long as rest of metathorax, rounded posteriorly. Coxae, femora, and front tibia with prominent scattered sensoria; tibiae basally differentiated. Aedeagus moderately inflated at base, slender toward apex, apical process sharply pointed, forming an acute angle with the main axis. Length of body excluding antennae 1.5 mm., length of antennae 0.41 mm., width of head 0.42 mm., wing expanse 2.35 mm.

Female. Cephalothorax yellowish brown, first sternite of abdomen with an irregular brownish patch, which is about as broad as long and tapers to a blunt point posteriorly. Cephalothorax longer than broad, angled at base of head and at mandibles, strengthened dorsally by longitudinal rodlike thickenings, margin of brood canal with a weakly defined thickening. Width of cephalothorax at spiracles 0.17 mm., width at base of mandibles 0.11 mm., width at base of head 0.18 mm., width at base of cephalothorax 0.15 mm., length from brood-canal opening to apex 0.11 mm., length from base of cephalothorax to apex 0.21 mm.

Holotype, male, and allotype, female, Granger, Utah, July, 1937 (D. Knowlton). Paratypes: One male and one female, same data as holotype; one male and three females, Turkey Creek, Arizona, June, 1933 (P. W. Oman); two males and six females, Vonda, Saskatchewan, Canada. Holotype and allotype to be deposited in United States National Museum, paratypes in collections of California Academy of Sciences and the author.

Hosts.—Athysanella utahne Osborne (Utah), *Flexamia flexulosa* Ball (Arizona), *Euscelis frigidus* Ball (Canada), and *Eibautiella affinis* G. and B. (Canada) (P. W. Oman determinations).

FIG. H

1. *Halictophagus oncometopiae* (Pierce), antenna.
2. *Halictophagus insularum* (Pierce), antenna.
3. *Halictophagus bidentatus* Bohart, antenna.
4. *Stenocranophilus quadratus* Pierce, antenna.
5. *Tridactylophagus mysorensis* Subramanium, male antenna (redrawn after Subramanium).
6. *Elenchus koebeli* (Pierce), male antenna.
7. *H. insularum*, female cephalothorax.
8. *S. quadratus*, female cephalothorax.
9. *H. oncometopiae*, female cephalothorax.
10. *Halictophagus mackayi* (Bohart), female cephalothorax.
11. *Halictophagus americanus* Perkins, female cephalothorax.
12. *T. mysorensis*, female cephalothorax.
13. *T. mysorensis*, first larva, lateral.
14. *T. mysorensis*, end of abdomen of first larva, ventral.
15. *S. quadratus*, female mandible.
16. *H. oncometopiae*, female mandible.
17. *T. mysorensis*, female mandible.
18. *H. insularum*, female mandible.
19. *H. oncometopiae*, aedeagus.
20. *H. mackayi*, aedeagus.
21. *S. quadratus*, aedeagus.
22. *H. oncometopiae*, male puparium cap, front view.
23. *Halictophagus barberi* (Pierce), aedeagus.
24. *Halictophagus membraciphaga* Subramanium, aedeagus.
25. *E. koebeli*, aedeagus.
26. *H. oncometopiae*, front leg.
27. *H. insularum*, front leg.
28. *E. koebeli*, male puparium cap, front view.
29. *H. mackayi*, front leg.
30. *H. membraciphaga*, front leg.
31. *E. koebeli*, male head and prothorax, lateral.
32. *E. koebeli*, male, dorsal.
33. *E. koebeli*, female cephalothorax and a portion of abdomen, ventral.
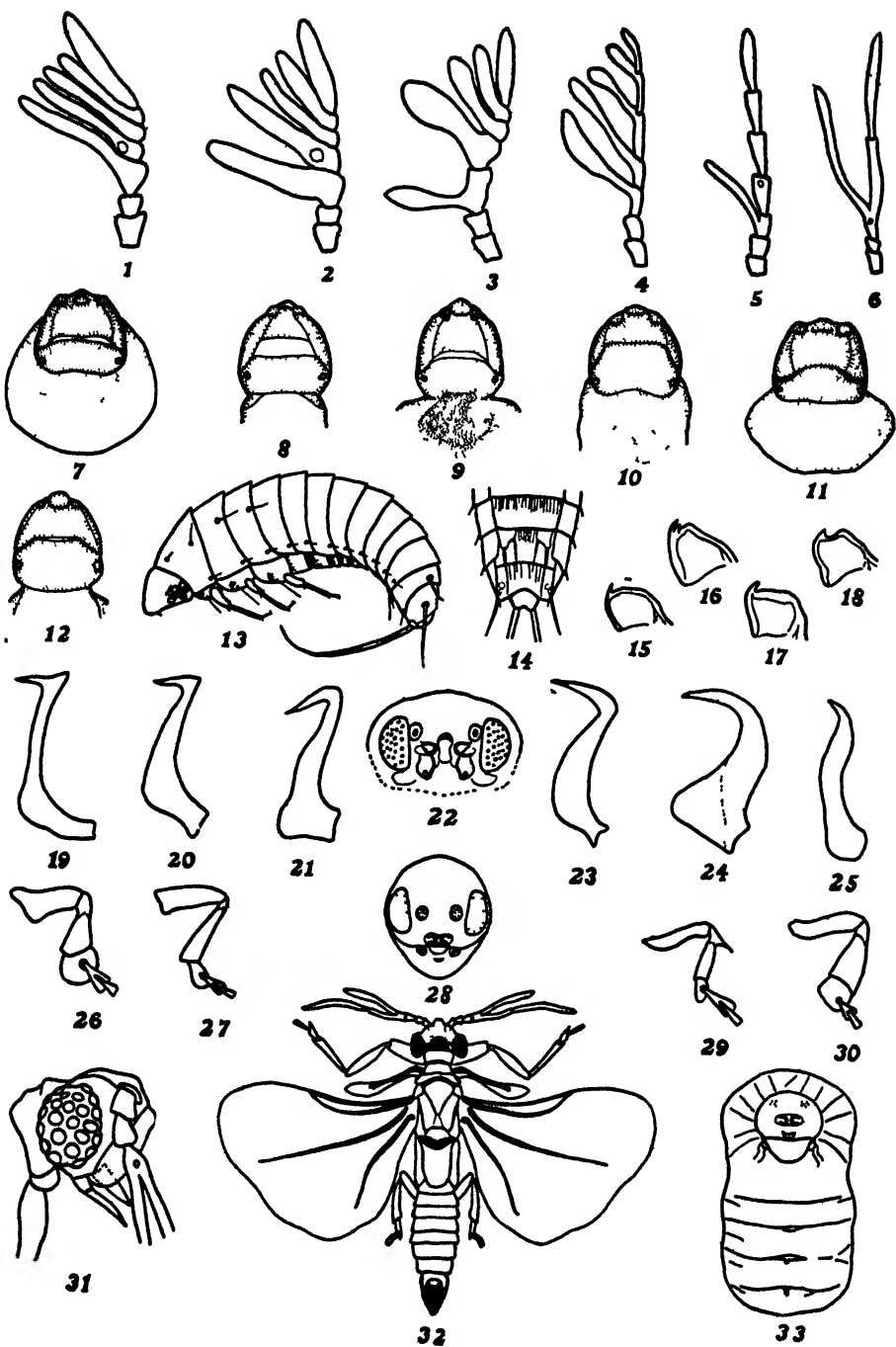
Fig. H.

Halictophagus oncometopiae (Pierce)
(Fig. H, 1, 9, 16, 19, 22, 26)

Dacyrtocara oncometopiae Pierce, 1918:473 (holotype, USNM).
Dacyrtocara undata Pierce, 1918:473 (holotype, USNM).

The sharp angle at the base of the front femur and the short prescutum are characteristic of the male. The female possesses two-toothed mandibles. *H. oncometopiae* was based by Pierce on a misidentified specimen of *Oncometopia undata* as host. Redetermination of the host material by P. W. Oman has cleared up this point.

Host.—Oncometopia undata Fabr.
*Distribution.—*Eastern North America.

Halictophagus americanus Perkins
(Fig. H, 11)

Halictophagus americanus Perkins, 1905:105 (holotype, USNM).
Agalliaphagus uhleri Pierce (nec Pierce, 1909), 1918:479 (holotype USNM).

Hosts.—Aceratagallia uhleri Van Duzee, *4-notata* (Prov.).
*Distribution.—*North America.

Halictophagus uhleri (Pierce)

Pentagrammaphila uhleri Pierce, 1909:169 (holotype, USNM).

This species is known only from the female holotype. It was placed by Pierce in the family Elenchidae but is a typical halictophagid. The cephalothorax is about as broad as long and the mandibles are one-toothed. The basal band is very large, the portion on the abdomen being as long as the cephalothorax.

Host.—Pentagramma vittifrons Uhler, "Dacota."

Genus *Stenocranophilus* Pierce
(Genotype *Stenocranophilus quadratus* Pierce)

Stenocranophilus Pierce, 1914:126, 1918:477.
Muirixenos Pierce, 1918:472.
Delphacixenos Pierce, 1918:475.
Delphacixenos, Ogloblin, 1925:172.
Delphacixenos, Ulrich, 1930b:19.

The genus is characterized by the elongate form of the antennae as opposed to the compact type of *Halictophagus*. The fifth segment is particularly long, being more than twice as long as broad. The aedeagus in the three known species is rounded rather than hooked apically. The mandibles are short and stout, and the terminal palpal segment is nearly cylindrical. *Stenocranophilus* is restricted to fulgorids and appears to be a connecting link between *Elenchus*, also parasitic on Fulgoridae, and *Halictophagus*, which is mainly found on Cicadellidae.

KEY TO THE MALES OF STENOCRANOPHILUS

1. Sixth antennal segment without a lateral prolongation; last antennal segment
   almost twice as long as sixth; Russia, Canada...............*anomalocerus* Pierce
   Sixth antennal segment with a lateral prolongation which is about as long as the
   segment proper; last antennal segment only slightly longer than sixth.............2
2. Last antennal segment slender, longer than the fifth; West Indies......*quadratus* Pierce
   Last antennal segment stout, shorter than the fifth; Java........*dicranotropidis* Pierce

Stenocranophilus anomalocerus (Pierce)

Delphacixenos anomalocerus, Pierce, 1918:475 (holotype, USNM).
Delphacixenos anomalocerus, Ogloblin, 1925:172.
Delphacixenos anomalocerus, Ulrich, 1930b:19.

Previously known only from the Palearctic region, this species has recently turned up in Canada. A specimen, collected on a fulgorid by Dr. Saunders of the University of Saskatchewan and sent to the author by Margaret MacKay, is very probably of this species. It should be noted that the antennae are not exactly as given in the figure of this species by Pierce (1918). The lateral prolongations of the third and fourth segments should be longer, and the fifth segment has a small but distinct lateral prolongation. The aedeagus is also somewhat in error. It is actually very similar to that of *dicranotropidis* although somewhat more inflated at the base.

The female has been described and figured by Ogloblin (1925). The mandibles are apparently two-toothed in contrast to the single-toothed condition in *quadratus*.

Hosts.—Delphacodes marginata (Fabr.) (after Ulrich), Russia; fulgorid species, undetermined, Saskatchewan, Canada.

Genus *Tridactylophagus* Subramanium
(Genotype *Tridactylophagus mysorensis* Subramanium)

Tridactylophagus Subramanium, 1932:43.

The antennae are the most reduced of any of the halictophagids (fig. H, 5). The genus is apparently most closely related to *Stenocranophilus* and also resembles *Elenchus* in some respects. A series of specimens was sent to the author by T. V. Subramanium, and the drawings of the male antenna, female cephalothorax, and first larva were made from this material. The single species is known only from India, parasitic on a gryllid.

Host.—Tridactylus nigraeneus Walker, Mysore State, India.

Genus of Uncertain Position

Colacina Westwood, 1877:185.

Described only from the male puparium in a species of *Epora* collected in Borneo.

Family ELENCHIDAE Perkins

Elenchinae Perkins, 1905:98.
Elenchoidea Pierce, 1908:76, 1909, 1911b, 1918.
Elenchidae Pierce, 1908:77, 1909, 1911b, 1918.
Elenchinae, Ulrich, 1930b:7.

The family as reconstituted contains only the genus *Elenchus*.

Genus *Elenchus* Curtis
(Genotype *Stylops walkeri* Curtis)

Elenchus Curtis, 1831:385.
Elenchus, Saunders, 1872:32.
Elenchus, Perkins, 1905:106, 1910:667.
Deinelenchus Perkins, 1905:107.
Elenchus, Pierce, 1908:81, 1909:165, 1911b:43, 1918:480.
Mecynocera Pierce, (nec J. C. Thompson, 1888) 1908:81, 1909:168.
Elenchoides Pierce, 1909:167, 1911b:45.
Deinelenchus, Pierce, 1909:170, 1911b:45.
Liburnenchus Pierce, 1918:481.
Elenchinus Pierce, 1918:481.
Pseudelenchus A. Ogloblin, 1925:173.
Elenchus, Ulrich, 1930b:19.
Pseudelenchus, Ulrich, 1930b:20.

The reduced wing venation, two-segmented tarsi, and four-segmented antennae of the male and the enlarged brood-canal opening and reduced thorax of the female are the outstanding characters of the genus. The general appearance and structural peculiarities are illustrated in fig. H, 6, 25, 28, 31–33.

Elenchus koebeli (Pierce)
(Fig. H, 6, 25, 28, 31, 32, 33)

Mecynocera koebeli Pierce, 1908:81, 1909:168 (holotype, USNM).

This species can be distinguished from *heidemanni* by the less pedunculate scutellum in the male. In *heidemanni* the scutellum is drawn out posteriorly into a long neck, whereas in *koebeli* it is almost triangular. From lack of evidence to the contrary it has been assumed that *koebeli* is distinct from European species.

Hosts.—Various species of *Liburnia*.
Distribution.—North America.

Elenchus heidemanni (Pierce)

Liburnenchus heidemanni Pierce, 1918:481 (holotype, USNM).
Elenchinus heidemanni Pierce (nec Pierce, 1918), 1918:481 (holotype, USNM).

The two species named by Pierce after Heidemann are apparently synonymous as well as homonymous, but the species is distinguished from *koebeli* by the characters given above.

Host.—*Megamelanus* species, Bay Ridge, Maryland.

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PLATE

PLATE 3

a. *Triosocera mexicana* Pierce, male.
b. *Pterotus obscuripennis* Lec., male.

a

b

NEW SPECIES OF LYGUS FROM CALIFORNIA
(HEMIPTERA, MIRIDAE)

BY

N. WARD STANGER

NEW SPECIES OF LYGUS FROM CALIFORNIA

(HEMIPTERA, MIRIDAE)

BY

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SIX NEW SPECIES of *Lygus* were revealed by a study of the collection at the California Academy of Sciences, in which all the holotypes are now deposited. On the basis of genital claspers (see fig. 1) these species belong to the *pratensis* group of Knight, as described in his revision of the genus (1917). The term
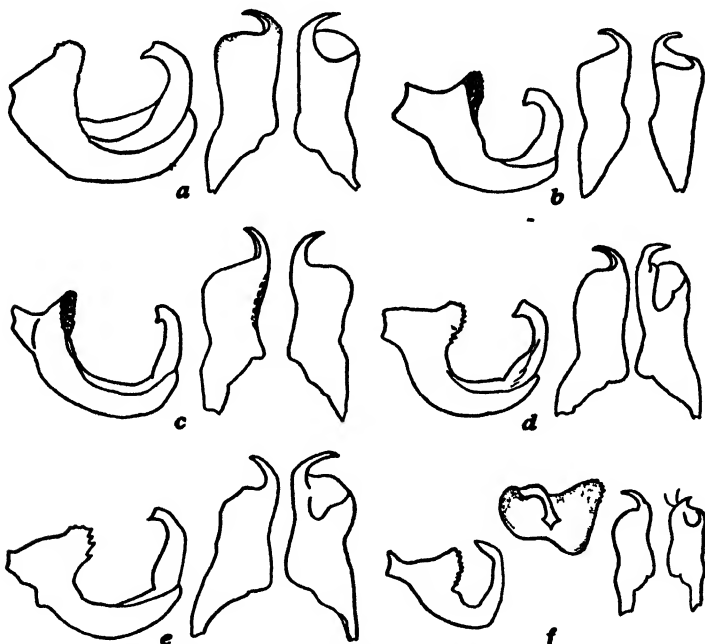
Fig. 1. Dorsal view of left and right, and internal face view of right genital claspers of *Lygus* (*a*) *dolichorhynchus*, (*b*) *regulus*, (*c*) *maculosus*, (*d*) *perplexus*, (*e*) *ravus*, and (*f*) *usingeri*, including also an internal face view of left clasper, showing its similarity to *L. nubilus* (Van Duzee) and *L. nubilatus* Knight. All × 150 *ca*.

gena, as used in this paper, includes the areas designated as gena and lora by Knight (1917). Length of body is measured from the greatest forward extension of the tylus, as seen in a single dorsal plane, to the apex of membrane. Length of rostrum is measured from its tip to the base at tip of tylus. The vertex is the area between inner margins of eyes in front of the transverse carina at apex of head. Width of head is measured between the outer lateral margins of the eyes. Width of pronotum is measured at the base between the lateral humeral angles. Length of antennal segments is measured between the distal and proximal joints of each segment; the first segment is measured from the point of greatest constriction to the joint between the first and second seg-

ments. Width of hemelytra is measured between the lateral margins at base of cuneus.

The writer is indebted to the late E. P. Van Duzee, of the Academy, for the loan of the specimens. R. L. Usinger contributed much helpful criticism of the manuscript.

Lygus regulus, n. sp.

Description.—Fulvous, with fuscous at basal angles of pronotum and spot at inner angles of calli; calli shining, with fuscous at apex. In general aspect *regulus* is nearest *pabulinus* Linnaeus but is less elongate, 3.0::4.8, narrower in total width, 4.3::7.0, and in width of pronotum at base, 3.7::5.3. They differ also in punctation on the pronotum, clavus, and corium which is coarse in *regulus* and fine in *pabulinus*. *L. pabulinus* is uniformly fulvous, some forms glaucus, while *regulus* is marked with fuscous on apex of corium, cuneus, and base of pronotum.

Head: bucculae, genae, juga, and tylus are yellow-brown; sutures between tylus, bucculae, genae, and juga are reddish; front and vertex yellow-brown with carina well-elevated; frontal transverse striae indistinct; eyes fuscous. Rostrum: attaining hind coxae; length 2.0 mm., proportion of segments one to four, 1.9:1.7:1.5:1.7. Antennae: first segment yellow-brown above, ferruginous below, length, .7 mm.; second segment red with apex fuscous, nearly equal to width of pronotum, length 2.5 mm.; third and fourth segments fuscous with base of third pale; pubescence over all segments yellow and appressed; length of third and fourth segments, 1.2 mm. and .80 mm. respectively; Pronotum: collum yellow-brown to fuscous; collar yellow-brown to yellow; calli yellow-brown; disk yellow, with spot behind inner posterior angles of calli, basal margins, and spot on posterior angles of disk, fuscous; sides uniformly yellow-brown, coarsely and deeply punctate, shining, pubescence sparse. Scutellum: fulvous to reddish-brown. Hemelytra: clavus uniformly reddish-fulvous with fuscous medially in some forms separated by pale claval vein; corium yellow-translucent with outline of abdomen showing through and fuscous at apex; embolium yellow-translucent with fuscous angles and apex; membrane lightly infumed to clouded with fuscous; clavus coarsely and closely punctate; corium not as heavily punctate, sparse yellow pubescence. Legs: coxae, trochanters, and femora, yellow-brown, with two apical annuli and extreme apical margin, red; tibiae yellow, with fuscous apex and claws. Abdomen: yellow-brown.

Female.—Similar to male.

Size.—Length 6.5 mm.; width (head) 1.4 mm., (pronotum) 2.6 mm., (hemelytra) 3.5 mm.

Holotype, male, no. 5015, and allotype, female, no. 5016, Calif. Acad. Sci., Ent., Kings River Canyon, Fresno County, California, July 4, 1910, by E. C. Van Dyke. Paratypes in the Calif. Acad. Sci. Female, Mount Eddy, California, elevation 9000 feet, July 28, 1918, by E. P. Van Duzee; one female, Colestin, Jackson County, Oregon, August 1, 1918, by E. P. Van Duzee; male, Fallen Leaf Lake, El Dorado County, California, July, 1931, by O. H. Swezey; male, Gold Lake, Sierra County, California, August 2, 1921, by C. L. Fox.

Lygus usingeri, n. sp.

Description.—Fulvous, with most of cuneus, collar, posterior margin of pronotum narrowly, and apex of scutellum, white; pronotal disk posteriorly, apex of corium, scutellum basally and laterally, and cuneus at base and apex, reddish brown. This species is closely allied to *nubilus* and *nubilatus*, but differs from both in its narrower body form; width of *usingeri* to *nubilus*, 2.6::3.0; to *nubilatus*, 2.6::3.0; length of *usingeri* to *nubilus*, 6.5::7.0; to *nubilatus* 6.5::7.5; second antennal segments, *nubilus* and *nubilatus* to *usingeri*, 2.0::1.8. Punctation of pronotum of *usingeri* is more widely separated than that of the other two species. Abdomen of *usingeri* is shining greenish-yellow, while that of *nubilatus* is pale with brown lateral stripe. *Nubilus* is much darker than either species. The male genital claspers show small, distinct differences.

Head: front reddish-brown with white median line from base of tylus to carina of vertex; carina white, distinct at base of vertex; white line extending across front between bases of antennae; rounded portion of tylus, white, mottled with reddish-brown; white lines at apices of eyes and extending ventrad along margins of eyes; eyes brown; apices of juga white, convex areas of genae white; bucculae white with black on posterior half of ventral margin. Rostrum: slightly to distinctly surpassing hind coxae; length 1.97 mm.; proportion of segments one to four, 12:12:10:13. Antennae: over half again as long as greatest width of pronotum, 71::44, proportion of segments one to four 12:29:18:12; first segment yellow; second segment yellow, thicker at apex with closely appressed, fine, yellow pubescence; third segment light yellow at base shading to black at apex; fourth segment fuscous, vestiture of fine yellow pubescence. Pronotum: basal half pale with suggestions of four reddish-brown lines extending from calli to base of pronotum; basal margin narrowly and collar, white; collar gray in some forms; calli fulvous, paler at anterior medial margin of calli; white line extending from anterior margin between calli to basal margin; covered with distinct, fuscous, setiferous punctures behind calli; the hairs short, pale, fulvous, and subappressed. Scutellum: mesoscutum, exposed equal to one-sixth of length of scutellum, reddish-brown with white sublaterally; bivittate with reddish-brown at middle of base separated by white vitta that widens at middle to include all of tip; outer margin reddish-brown except for white tip and areas separating vittae. Sternum: ventrally and extending to near base of second coxae, black; pleural portion reddish-brown. Hemelytra: clavus pallid with reddish-brown along commissure and at tip; corium pallid except for reddish-brown area extending from tip of clavus to internal basal margins of cuneus; cuneus clear except for red at tip and extending one-third length of internal margin, also at outer basal angle of cuneus narrowly, red; fracture deep; clavus and corium finely punctate and with closely appressed yellow pubescence; membrane infumed, clear areas opposite tips of cuneus posteriorly, along margins of cuneus at tip, and extending parallel with red area of cuneus; veins yellowish to reddish. Legs: pale, reddish-brown at apices of tibiae and black at tips of tarsi; claws dark brown; hind femora extending from middle to apices, reddish with two pale rings near apices; hind tibiae pale with black spines and yellow pubescence; tarsi pale. Abdomen: reddish laterally with white spots at spiracles; gray ventrally; ninth segment entirely reddish.

Female.—Generally more pallid with reddish; head yellow; pronotum more pallid, calli pallid in some with a trace of red over pronotum in others; posterior margin white; red on mesoscutum and scutellum in place of reddish-brown of male; bucculae pale; first and second antennal segments yellow; third and fourth similar to male; legs yellow with two distinct annuli near apices of hind femora, with a trace of red from middle of femora to first annulus; sternum more uniformly reddish-yellow; abdomen yellow, a trace of red ventrally and including all of ninth segment; female more robust than male.

Size.—Male: length 4.0 mm.; width (head) 1.1 mm., (pronotum) 2.2 mm., (hemelytra) 2.5 mm. Female: length 4.6 mm.; width (hemelytra) 2.6 mm.; length rostrum 1.9 mm. (shorter than male).

Holotype, male, no. 5017, Calif. Acad. Sci., Ent., allotype, female, no. 5018, Calif. Acad. Sci., Ent., and four male and four female paratypes; collected at 5907 feet elevation along the trail near Nevada Fall, Yosemite National Park, California, August 14, 1938, by R. L. Usinger. Paratypes in the collections of R. L. Usinger and the writer.

Lygus perplexus, n. sp.

Description.—Calli reddish-fuscous, with small yellow-brown area near inner margins and black ray extending posteriorly from inner angles; head marked with fuscous to piceous. *L. perplexus* in general aspect appears to be a smaller duplicate of *L. aeratus* Knight. Width of *perplexus* to *aeratus*, 3.7::4.0; length of *perplexus* to *aeratus*, 8.5::9.0; width of pronotum at base and length of second antennal segment in *perplexus* to *aeratus*, 3.3::3.5 and 2.5::3.0, respectively. Punctation on pronotum of *aeratus* coarser and more closely placed than on *perplexus. Aeratus* appears more robust and darker than *perplexus.* Scutellum of *aeratus* uniformly fuscous to black, as contrasted to reddish scutellum of *perplexus.*

Head: bucculae black with yellow-brown ventral margin and median area; gena fuscous to piceous with yellow-brown spot below eyes; jugum pale on apex with yellow-brown at base and fuscous to piceous between; tylus fuscous to piceous near apex with yellow-brown at base; front with five striae and two fuscous to piceous lines arising from a similarly colored area dorsal to antennal bases, one pair of lines extending from antennal bases to a spot fuscous to piceous in color on vertex, second pair of lines extending along margins of eyes and pointing inward at fuscous spot on vertex; eyes mottled with fuscous and pale; carina distinctly yellow. Rostrum: attaining hind coxae; length 2.9 mm.; proportion of segments one to four as 1.5:1.3:1.0:1.5. Antennae: first segment ferruginous above with piceous below, broad annulus at its base and narrow apical anulus, black; length .6 mm.; second, length 1.85 mm., fuscous; third and fourth segments missing. Pronotum: collum black; collar yellow-brown to fuscous behind eyes; anterior margin of pronotum strongly arcuate, yellow before calli and at ultimate anterior angles; calli black with fuscous spot extending inward from inner margins and broad black band extending from anterior lateral margin to anterior margin of disk; black ray from inner basal angle of each callus; black at basal angles; disk fulvous, deeply and coarsely punctate, shining, sparsely pubescent; sides of disk piceous between dark fulvous dorsal margin and fulvous ventral margin, posterior margins of sides also dark fulvous. Scutellum: reddish, pale at tip and two basal dashes lateral to broad black basal median area. Sternum: black, yellow-brown on pleura. Hemelytra: clavus reddish-fuscous, very narrowly fuscous on margins adjacent to scutellum and along commissure of hemelytra, coarsely and deeply punctate to rugose with very sparse yellow pubescence; corium brownish-translucent with dark outline of abdomen showing through; thickened margin of corium posterior to apex of clavus pale, pubescence sparse; embolium yellow-brown translucent, fuscous on extreme outer margin; cuneus yellow-brown translucent, fuscous on extreme outer margin, reddish on inner margin and in arc across base to beginning of fracture; apex darker in small area along vein at apex of large cell. Legs: coxae and trochanters black; femora fuscous to reddish at apex; hind femora yellow-brown to reddish on basal half, reddish on apical half, broad reddish apical band and fuscous annulus on extreme apical margin; hind tibiae yellow-brown, with spot at knee, annuli below, apex, and spines, fuscous; tarsi yellow-brown, apex and claws, fuscous. Abdomen: piceous ventrally to dark fuscous laterally, spiracles pale.

Size.—Length 5.0 mm.; width (head) 1.3 mm., (pronotum) 2.7 mm., (hemelytra) 3.5 mm.

Holotype, male, no. 5019, and allotype, female, no. 5020, Calif. Acad. Sci., Ent., and two male and four female paratypes, Shasta Springs, California, June 20, 1920, by C. L. Fox.

Lygus ravus, n. sp.

Description.—Gray-brown with black and pale stripes alternating on pronotum; cuneus translucent, margined with brownish. *L. ravus* is similar to *L. humeralis* Knight except for size of scutellum. Width, 1.7::2.0, respectively; second antennal segment, 2.3::2.0; length from tylus to apex of cuneus, 7.3::8.0. Male genital claspers are distinct.

Head: gula, bucculae, and genae, black; jugum with wide black band across middle from base of antennae to margins of tylus; tylus black on apex with fuscous above, extreme apical margin pale; front marked with a fuscous triangle, base arises from lines across apex of front between bases of antennae; apex of triangle reaches center of vertex and ends in fuscous spot; fuscous line extends from base of antennae along margins of eyes and point to apex of triangle; carina pale, slightly elevated and posteriorly arcuate; eyes mottled with pale and brown. Rostrum: attains hind coxae; length 1.6 mm. Antennae: first segment fuscous to piceous, extreme apical margin pale, length .5 mm.; second segment fuscous with piceous on base and apex, length 1.8 mm.; third fuscous, length 1.0 mm.; fourth missing; all with fine pale pubescence. Pronotum: collum black; collar flattened and broadened at vertex, strongly posteriorly arcuate, pale to inner margins of eyes, fuscous behind eyes, narrowly yellow on anterior margin of pronotum before calli and between; calli and anterior angles black with yellow-brown spot on inner half of calli, two black rays behind each calli, and black from anterior angles to posterior angles, pale between rays; basal half of prono-

tum black with extreme basal margins pale; punctation deep and scattered; pubescence very sparse, yellow; lateral edges of disk, ventral and posterior margins of sides, pale; rest of side black and smooth. Sternum: black with pale at apex of second coxae. Scutellum: transversely rugose, fuscous with pale median vitta widening to include all of tip and two pale dashes on either side at base. Hemelytra: clavus gray-brown, darker in middle and gray in region of commissure of hemelytra; apex of clavus and narrow margin adjacent to scutellum and commissure of hemelytra, fuscous, with claval vein pale to grayish brown in regions of these shades; coarsely and closely punctate with very sparse, pale pubescence; corium gray-brown translucent, adjacent to clavus and apex, and fuscous along cubitus, widening to include base of corium, darkest nearest cubitus, white posterior to apex of clavus on margin of corium, dark dorsum of abdomen shows through, translucent from here to inner margin of embolium with fuscous at apex in V formed by marginal vein; embolium gray at base, translucent to apex, extreme outer margin black; cuneus translucent with fuscous to piceous on extreme outer margin, apex, and broadly across base, cubitus white from fracture to membrane; membrane fuscous at base; posterior to anal vein, fuscous at apex of large cell in narrow band parallel to vein. Legs: coxae black; trochanters fuscous with lighter margins; femora fuscous lighter on dorsal side; hind femora thrice annulated with yellow-brown at apex, extreme apical margin fuscous; hind tibiae yellow with spot at knee, annulus below and apex, fuscous; spines fuscous; tarsi yellow with brown on apical half of third segment. Abdomen: black with dimple in second and third segments laterally near dorsum; sparsely covered with pale pubescence.

Size.—Length 5.2 mm.; width (head) 1.2 mm., (pronotum) 2.3 mm., (hemelytra) 3.1 mm.

Holotype, male, no. 5021, Calif. Acad. Sci., Ent., Selkirk Range, British Columbia, July, 1908, by J. C. Bradley. A female specimen from Shasta Springs, California, June 20, 1920, by C. L. Fox, is also in the Calif. Acad. Sci., Ent., collection.

Lygus maculosus, n. sp.

Description.—Yellow-brown mottled with fuscous, pubescence prominent, yellow in yellow-brown areas and brown on fuscous areas of hemelytra, cuneus translucent with dark ferrugineous on basal outer angle and apex, inner margin red. *L. maculosus* is similar to *L. convexicollis* Reuter, differing in size as follows: width of pronotum of *maculosus* to *convexicollis*, 3.3::4.2; length of pronotum of *maculosus* to *convexicollis*, 1.8::2.2; length of *maculosus* to *convexicollis*, 9.8::11.0; width of *maculosus* to *convexicollis*, 5.0::4.4. *Maculosus* has patches of white pubescence over hemelytra while *convexicollis* has sparser, uniformly yellow pubescence over hemelytra.

Head: bucculae and juga, yellow-brown, broadly fuscous at sutures; genae and gula, fuscous; juga with fuscous band across middle from base of antennae to margins of tylus; tylus yellow-brown with fuscous band at apex; front with six poorly defined striae, with a suggestion of a fine, fuscous line from base of antennae across apex of face, fuscous lines extending from bases of antennae to vertex and jutting inward; vertex yellow-brown with distinct carina; eyes brown. Rostrum: attaining hind coxae; length 2.5 mm.; proportion of segments one to four, 1.7:2.0:2.0:1.3. Antennae: first segment reddish-brown dorsally, fuscous ventrally, length .75 mm.; second segment fuscous at base, followed by yellow-brown, which gradually shades into fuscous at apex, length 2.0 mm.; third segment fuscous, length 1.0 mm.; fourth segment fuscous, length .6 mm. Pronotum: collum black; collar pale, flattened, broad and posteriorly arcuate; ultimate anterior angles flavous, anterior margins of pronotum before calli, yellow; black crescent around anterior and lateral sides of calli, enclosing their yellow-brown centers; black ray behind each callus at internal angles, and black extending in a wide band from anterior angles of calli to anterior margin of pronotum; disk darker flavous with black at posterior angles, the extreme posterior margin pale; pubescence very sparse and golden, punctation coarse and heavy, lighter on basal half. Scutellum: fuscous with yellow-brown median vitta extending to include tip with black area basal and lateral to vitta, heavily and transversely rugose, pubescence sparse; in lighter forms scutellum yellow with two short black basal vittae and reddish-brown lines

parallel to sides. Sternum: fuscous to fulvous on sides. Hemelytra: clavus fuscous narrowly along margin adjacent to scutellum and commissure of hemelytra, remainder of clavus mottled with fuscous and yellow-brown with sparse yellow pubescence; corium mottled with fuscous, interior yellow-brown to brachium, with mingled pale yellow and fuscous pubescence, apex fuscous, exterior to brachium translucent, with fuscous at apex; embolium yellow-brown with fuscous on extreme outer margin and apex; cuneus reddish translucent with dark ferruginous in outer basal angle and apex, inner margin red; membrane clouded with fuscous, narrowly pale at margins of cuneus, fuscous at apex anterior to anal vein; veins red. Legs: coxae marked with pale and fuscous; trochanters fulvous with three apical annuli on distal half, third annulus on extreme apical margin; tibiae yellow with spines, spot at knee, streak below and apex fuscous; tarsi and claws fuscous. Abdomen: fuscous ventrally, eighth and ninth segments yellow, broad yellow band laterally with large fuscous rectangular areas below, pale spiracles, pubescence sparse, pale.

Size.—Length 6.6 mm.; width (head) 1.5 mm., (pronotum) 2.6 mm., (hemelytra) 3.5 mm.

Holotype, male, no. 5022, Calif. Acad. Sci., Ent., Lagunitas, Marin County, California, August 7, 1921, by E. P. Van Duzee. Allotype, female, no. 5023, San Francisco, California, June 24, 1925, by H. H. Keifer; female, paratype, Mount Tamalpais, Marin County, California, June 23, 1918, by E. P. Van Duzee; in same collection.

Lygus dolichorhynchus, n. sp.

Description.—Dark reddish-brown, black scutellum with pale apex. Color patterns of *L. dolichorhynchus* and *convexicollis* are similar except that the former lacks reddish aspect. Punctation of pronotum is coarser and more closely placed in *dolichorhynchus*. Scutellum of *convexicollis* differs in having lateral pale vitta alternate with black vitta and pale tip, while *dolichorhynchus* has black scutellum with pale tip. Length of antennae of *dolichorhynchus* to *convexicollis*, 8.0::8.4; pronotal width, 3.0::2.5; length, 6.0::5.3.

Head: tylus reddish-brown, fuscous at apex; bucculae piceous with pale on ventral margin; gena piceous with pale spot immediately below eye; jugum pale with piceous band across middle; eyes reddish-brown, piceous line extends from base of antennae along margins of eyes to vertex; front brownish with indistinct transverse striae; carina well-elevated, yellow. Rostrum: extends to posterior margin of seventh abdominal segment; length 3.4 mm. Antennae: first segment reddish-brown above, piceous below, length .7 mm.; second, third, and fourth segments fuscous to piceous with pale pubescence, lengths 1.95 mm., 1.0 mm., .6 mm., respectively. Pronotum: collum black; yellow and reddish-brown behind eyes; stricture arcuate posteriorly; yellow before calli; calli ferrugineous with black on outer portions and small black spot at posterior angles, with red ray suggested extending posteriorly; humeral angles of pronotum piceous; disk ferrugineous, heavily, coarsely punctate, shining with sparse pale pubescence; extreme basal margin pale; sides reddish-brown with pale on ventral margin, black at anterior angles along coxal cleft. Sternum: piceous with fuscous on sides and pale at base of second coxae. Scutellum: black with pale apex. Hemelytra: clavus rich red-brown to fuscous, coarsely punctured and sparse, pale pubescence; corium reddish-brown translucent, dark dorsum of abdomen shows through; embolium yellowish-brown to fuscous with fuscous on extreme margin and apex before cuneus; cuneus yellow-brown translucent with fuscous at outer and inner basal angles and apex, inner margin red; membrane lightly infumed with fuscous, darker at apices of areola, veins reddish. Legs: coxae black, trochanters pale at margins; femora fuscous, first and second annulated at apices, with broad fuscous to piceous bands; hind femora with broad medial band and two indistinctly defined apical annuli and extreme apical margin fuscous; tibiae yellow-brown to fuscous with fuscous spot at knee and broad band below, spines and apex fuscous; tarsi yellow-brown with apical segment and claws fuscous. Abdomen: black with pale at spiracles and lateral pale band suggested.

Size.—Length 6.5 mm.; width (head) 1.7 mm., (pronotum) 2.6 mm., (hemelytra) 3.4 mm.

Holotype, male, no. 5024, Calif. Acad. Sci., Ent., Mill Valley, Marin County, California, March 21, 1926, by E. P. Van Duzee.

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  1917. Cornell Univ. Agr. Exp. Sta. Bull. 391:555–645, 1 pl., 208 figs. in text.

SYSTEMATICS OF THE MELOID GENERA HORNIA AND ALLENDESALAZARIA (COLEOPTERA)

BY

E. GORTON LINSLEY

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THE FIRST SPECIES of *Hornia* was discovered by C. V. Riley in 1887, and the genus has since attracted interest as one of the most remarkable groups of North American Meloidae. Unfortunately, however, the secretive and sub-
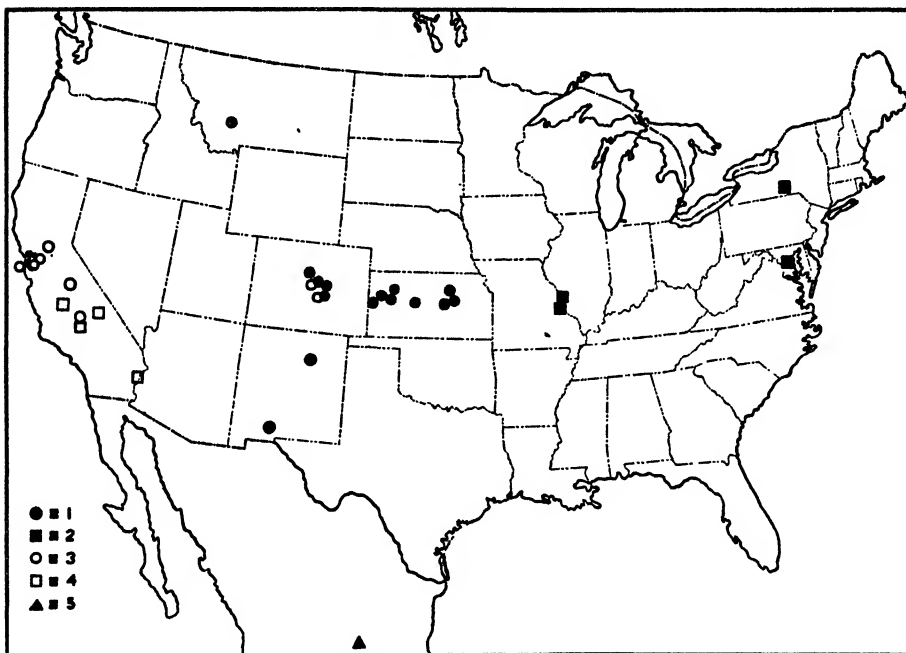
Map. 1. Distribution of Genus Hornia: (1) *Hornia neomexicana* (Cockerell); (2) *H. minutipennis minutipennis* Riley; (3) *H. minutipennis occidentalis* Linsley; (4) *H. boharti* Linsley; (5) *H. mexicana* Dugès.

terranean habits of the various species have made them very rare in collections. This fact, together with the degenerate and variable characteristics of the adults, has resulted in confusion and synonymy and a general lack of understanding of the species. At present, the group contains four species, including the new one described here, and two subspecies. The genus is distributed from the Atlantic to the Pacific, but the center of abundance for the species appears to be in western United States (see map 1).

The genus *Allendesalazaria* was proposed by Escalera in 1910 for a species from northern Africa. However, the name was quickly suppressed by Cros as a synonym of *Hornia* and has since been the subject of intermittent controversy. As will be shown, the resemblance between *Hornia* and *Allendesalazaria* appears quite superficial.

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Genus *Hornia* Riley

Hornia Riley, 1877, Trans. Acad. Sci. St. Louis, 3:564; LeConte and Horn, 1883, Smithson. Misc. Coll., 507:419; Dugès, 1886, Bull. Soc. Zool. France, 11:579; Dugès, 1889, An. Mus. Michoacana, 2:11; Champion, 1911, Entom. Mo. Mag., 47:16; Wellman, 1911, Entom. News, 22:16; Champion, 1911, Entom. News, 22:132; Cros, 1913, Bull. Soc. Hist. Nat. Afr. Nord, 4:42; Parker and Böving, 1924, Proc. U. S. Nat. Mus., 64(23):32; Van Dyke, 1928, Univ. Calif., Publ. Entom., 4:402; Mickel 1929, Entom. News, 40:6–7.

Leonia Dugès, 1889, Insect Life, 1:211; Dugès, 1889, An. Mus. Michoacana, 2:5, 15, 112; Champion, 1892, Biol. Centr. Amer., Coleopt., 4(2):371; Cockerell, 1899, Psyche, 8:416.

Leonidia Cockerell, 1900, Psyche, 9:11; Wellman, 1911, Entom. News, 22:16; Mickel, 1928, Entom. News, 39:41.

Adult.—Head wider than pronotum, subtriangular, deflexed, suddenly constricted posteriorly, posterior margin nearly straight, neck distinct; clypeus transverse, apex broadly emarginate; labrum large, transverse, apex subtruncate or broadly, shallowly emarginate, dorsal surface feebly concave; mandibles prominent, broad at base, outer margin evenly arcuate, inner margin nearly right angular but with the angle rounded, apices slender, extending beyond labrum, acute in fresh examples; maxillae with outer lobe short; maxillary palpi elongate, four-segmented, first segment short, second segment elongate, proportions of third and fourth segments variable; labial palpi three-segmented, ultimate segment longest; antennae ten- or eleven-segmented, segments submoniliform, flattened, variable in shape and proportions; eyes small, narrow, transverse, finely facetted. Pronotum as wide as or wider than long, subquadrate to subcordiform, convex; scutellum cordiform nearly as long as broad; coxae prominent, conical, anterior pair contiguous, intermediate pair overlapping posterior pair; legs slender, femora moderately robust, tibiae slender, spurs short, tarsi narrow, spinulose, claws simple or with an inner spine. Elytra greatly abbreviated, squamiform, suboval, at most only partly covering first abdominal tergite; wings rudimentary or absent. Abdomen large, saclike, oval or elongate oval, segments membranous or semicorneous; eighth sternite longitudinally cleft in male, entire or feebly emarginate in female.

Primary larva.—Head obcordiform, nearly as long as wide, broadly truncate in front, widest behind the middle; epicranial and frontal sutures distinct; clypeus and labrum fused with frons; labial palpi short, two-segmented; ocelli placed just behind middle of head, the pairs close together; antennae nearly one-third as long as head, apical seta long, slender; mandibles multidentate with from five to nine (rarely four to ten) teeth. Thorax as large as or nearly as large as abdomen, middorsal suture distinct on all three segments. Abdomen tapering apically; spiracle on first segment subequal to that of mesothorax, remainder smaller; spiracle bearing process of eighth tergite scarcely longer than basal width, apex obtuse; ninth segment with a pair of short, fine, apical setae which are distinctly shorter than the segment. Femoral setae fine, moderately short; tarsus about one-half as long as tibia, slender, claw-shaped with two long basal setae about two-thirds as long as tarsus.

Genotype.—*Hornia minutipennis* Riley (monobasic).

This genus is distinct among the adult American Nemognathinae on the basis of the form of the head, squamiform elytra, saclike and semimembranous abdomen, and structure of the tarsal claws. The primary larvae may be recognized by the truncate head, short spiracle-bearing processes of eighth abdominal tergite, and short, fine caudal setae. Parker and Böving (1924:32) state that the larvae have one well-developed, almost ventral tarsal seta, but this is apparently in error.

<div align="center">KEY TO THE SPECIES OF HORNIA</div>

<div align="center">ADULT MALES[1]</div>

1. Basal spine of tarsal claw short or absent, at most attaining middle of claw...........2
   Basal spine of tarsal claw long, conspicuous, at least attaining apical three-fourths of claw; head, thorax, and legs dominantly black or piceous, elytra fulvous; pubescence short, black, that of legs about one-half as long as greatest width of tibiae; abdominal tergites and sternites almost entirely corneous, heavily pigmented, black; antennae nearly attaining elytral apices. 13–15 mm. New Mexico, Kansas, Colorado.....................................*neomexicana*

2. Pubescence long, coarse, black, that of legs longer than greatest width of tibiae, that of abdomen more or less evenly distributed; head, thorax, and legs black, elytra rufous; tergites and sternites with a single, transverse, black, scelortized plate; antennae attaining elytral apices; tarsal claws simple. 7.5–11 mm. California ....*boharti*
   Pubescence short, dark brownish, that of legs about one-half as long as greatest width of tibiae, that of abdomen more or less confined to transverse tergal and sternal bands; head, thorax, and legs rufous or pale ferrugineous, elytra testaceous; tergites and sternites with a pair of rectangular, black, sclerotized plates; antennae attaining only base of pronotum; tarsal claws simple or with a short inner spine...3

3. Claws simple; tergal bands heavily sclerotized distinct on all segments. 14–16 mm. Eastern North America...........................*minutipennis minutipennis*
   Claws with short inner spine; tergal bands moderately sclerotized, those of first and second tergites feeble or indistinct. 14–16 mm. Western North America
   <div align="right">*minutipennis occidentalis*</div>

<div align="center">ADULT FEMALES[1]</div>

1. Basal spine of tarsal claw long, conspicuous, attaining apical three-fourths of claw 2
   Basal spine of tarsal claw, if present, attaining only middle of claw.................3

2. Head, thorax, and legs ferrugineous; last segment of maxillary palpi at least twice as long as penultimate segment; third antennal segment much larger than second, apex oblique, produced externally. 11 mm. Mexico.............*mexicana*
   Head, thorax, and legs dominantly black or piceous; last segment of maxillary palpi less than twice as long as penultimate segment; third antennal segment but little larger than second, apex truncate, not produced externally. 13–16 mm. New Mexico, Kansas, Colorado.....................................*neomexicana*

3. Pubescence long, coarse, black, that of legs longer than greatest width of tibiae, that of abdomen more or less uniformly distributed; head, thorax, and legs black, elytra rufous, abdomen often with vague, transverse, dark tergal bands; tarsal claws simple. 8–12 mm. California...............................*boharti*

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[1] Coloration and measurements are based on fresh material. Dry specimens are usually from one to three millimeters shorter with the abdominal segments distorted by shrinkage. For comparative purposes specimens should be preserved in liquid media or subjected to some such treatment as that suggested by Mickel (1928a).

Pubescence short, dark brownish, that of legs about one-half as long as greatest
width of tibiae, that of abdomen more or less confined to transverse tergal and
sternal bands; head, thorax, and legs rufous or pale ferrugineous, elytra testa-
ceous; tarsal claws simple or with a short inner spine.............................4
4. Tarsal claws simple. 14–16 mm. Eastern North America......*minutipennis minutipennis*
   Tarsal claws armed with a short inner spine. 15–17 mm. Western North America
   minutipennis occidentalis

PRIMARY LARVAE

1. Spiracle-bearing processes of eighth abdominal tergite separated by distinctly
   more than their basal widths...2
   Spiracle-bearing processes of eighth abdominal tergite separated by less than
   their basal widths...3
2. Mandibles bearing five (rarely four or six) teeth. New Mexico, Kansas, Colorado
   neomexicana
   Mandibles bearing nine (rarely eight or ten) teeth. California.................*boharti*
3. Mandibles bearing eight teeth; ultimate segment of maxillary palpi distinctly
   longer than penultimate. Eastern North America..........*minutipennis minutipennis*
   Mandibles bearing six (rarely seven) teeth; ultimate segment of maxillary palpi
   scarcely longer than penultimate. California..............*minutipennis occidentalis*

Hornia mexicana Dugès

Hornia mexicana Dugès, 1886, Bull. Soc. Zoöl. France, 11:579.
Leonia rileyi Dugès, 1889, Insect Life, 1:221, f. 47; Dugès, 1889, An. Mus. Michoa-
   cana, 2:5, 27, 112, pl. 1; Champion, 1892, Biol. Centr.-Am., Coleopt., 4(2):371;
   Cockerell, 1899, Psyche, 8:417 (*new synonymy*).
Leonidia rileyi, Mickel, 1928, Entom. News, 39:40, f. 3.
Hornia rileyi, Mickel, 1929, Entom. News, 40:7.

Female.—Color more or less dark ferrugineous; integument covered with stiff hair or
black setae. *Head* trapezoidal, a little wider than thorax, surface strongly depressed at
middle, ferrugineous; antennae stout, longer than head, punctulate and pubescent, first two
segments ferrugineous, remainder black, scape claviform, longer and thicker than other
segments, second segment transverse conical, one-half the size of scape, third segment coni-
cal, thinner and longer than second segment, intermediate segments tending to become
connate; labrum punctate, hairy, ferrugineous; epistoma punctulate, ciliate, ferrugineous.
Pronotum strongly transverse, one and one-third times wider than long, slightly narrowed
posteriorly, side margins nearly straight, anterior angles strongly rounded, posterior angles
less so, base slightly margined and sinuate; dorsal channel obsolete; surface shining, punc-
tate, ferrugineous, covered with black hairs; scutellum large, slightly transverse-triangular,
rounded at tip, punctate, black. *Legs* ferrugineous, covered with black hairs; femora slender,
without silky emargination; tarsal claws reddish, provided on the underside with a long,
straight, acute spine attaining three-fourths the length of the claw. *Elytra* nearly reaching
middle of first abdominal segment; surface coriaceous, rugose, punctate, testaceous, covered
with black hairs; wings absent. *Abdomen* shining and pubescent, very little inflated and
in no way baggy (en besace); segments entirely subcorneous but less so ventrally; last two
segments black, remainder dark brown with ferrugineous borders. Length 11 mm., breadth
3 mm.

Type locality.—Guanajuato, Mexico.
Host.—*Anthophora* sp. (Dugès, 1889)

The above description has been extracted and rearranged from those of Dugès (1889*a*,
b, *c*), with the omission of generic characters and those of other higher categories.

This species has generally been referred to under the name of *rileyi* Dugès
(1889) but an older and apparently valid name is available in *Hornia mexi-
cana* (1886) of the same author. Dugès first referred the species to *Hornia*

but later, after concluding that it was not congeneric with *minutipennis* Riley, he proposed both a new generic and a new specific name. The former, pre-occupied by *Leonia* Gray, was renamed *Leonidia* by Cockerell (1900). More recently, both Van Dyke (1928) and Mickel (1929) have shown that *Leonidia* is synonymous with *Hornia*. The specific name *rileyi* must also fall into synonymy since on Dugès' own statement his description was based on the same individuals previously called *Hornia mexicana*.

Apparently, *Hornia mexicana* has not been definitely recognized since the time of Dugès, although it may possibly be the same as *neomexicana* Cockerell. The latter species was separated mainly on the basis of antennal and palpal differences indicated in Dugès' figures. However, there are marked discrepancies between the figures of these structures given by Dugès (1889*a* and 1889*b*). The tarsal claws appear to be more correctly drawn in the latter publication. This may also be true of the third antennal segment, which is described as "conical" but shown in one publication (1889*a*) as an asymetrical structure with the inner angle produced. Likewise, the last segment of the maxillary palpi is represented as three times as long as the penultimate (1889*b*) or twice as long (1889*a*). In view of these discrepancies and the fact that the drawings in *Insect Life* appear to be redrawn from sketches supplied by Dugès, we are inclined to afford little significance to them for specific recognition.

Hornia neomexicana (Cockerell)
(Figure 1*g*)

Leonia neomexicana Cockerell, 1899, Psyche, 8: 416.
Leonina neomexicana, Schwarz, 1904, Proc. Entom. Soc. Wash., 6: 22.
Leonidia neomexicana, Fall & Cockerell, 1907, Trans. Am. Entom. Soc., 33: 209;
      Mickel, 1928, Entom. News, 39: 41, fig. 1.
Hornia neomexicana, Van Dyke, 1928, Univ. Calif. Publ. Entom., 4: 403; Mickel,
      1929, Entom. News, 40: 1–7; Hicks, 1934, Univ. Colo. Studies, 21: 265, fig. 1.
Hornia gigantea Wellman, 1911, Entom. News, 22: 16; Williams & Hungerford, 1914,
      Entom. News, 25: 1, pl. 1.
Leonidia anthophorae Mickel, 1928, Entom. News, 39: 38, fig. 2.

Adult Male.—Color of head, thorax and legs black or dominantly black, occasionaly tinted with ferrugineous, elytra fulvous, abdomen subcorneous, dark brown with narrow pale margins on tergites and sternites; integument shining, clothed with short, moderately numerous, coarse, black hairs. *Head* wider than pronotum, usually distinctly so, integument black or piceous, frons often tinted with ferrugineous, setae coarse, erect, black, about as long as greatest width of antennal segments, punctures coarse, distinct, but irregularly spaced; antennae ten- or eleven-segmented, surpassing the base of the pronotum, third segment usually more or less equilateral and but little larger than second segment; clypeus sparsely punctured and pubescent; labrum more densely punctured and clothed with coarse black setae; maxillary palpi with ultimate segment usually but little longer than penultimate segment, at most less than twice as long. *Pronotum* varying from a little wider than long to nearly one and one-third times as wide as long, basal margin elevated; surface irregularly punctured, punctures large, sparse over anterior half, very much scattered posteriorly; pubescence similar to that of head; scutellum cordiform, shining, a little wider than long. *Legs* black or piceous, clothed with coarse, erect, black setae about one-half as long as greatest width of tibiae; tarsal claws ferrugineous, armed with a long, slender, inner spine which reaches at least to apical three-fourths of claw. *Elytra* nearly attaining apical margin of first abdominal tergite; surface, rugose, punctured, clothed with coarse, black

hairs. *Abdomen* saclike, elongate-oval; segments subcorneous, piceous or dark brown, apical margins narrowly testaceous; tergites sparsely clothed with erect black hairs, sternites four to seven with a transverse band of dense, erect, black setae. Length 13–15 mm.

Adult Female.—Color frequently more ferrugineous than male; antennae reaching to about middle of pronotum; abdomen larger, segments less heavily sclerotized, sternites two to six submembraneous at middle, seventh and eighth sternites corneous. Length 14–15 mm.

Primary Larva.—Mandibles bearing five (rarely four or six) teeth; maxillary palpi with ultimate segment distinctly longer than penultimate segment; eighth abdominal tergite with spiracle-bearing processes separated by more than basal width.

Type locality.—Mesilla, New Mexico.

Hosts.—*Anthophora vallorum* (Ckll.) (Cockerell, 1899); *Anthophora bomboides neomexicana* Ckll. (Cockerell, 1905, Hicks, 1926); *Anthophora occidentalis* Cress. (Wellman, 1911, Williams and Hungerford, 1914, Mickel, 1928).

Recorded distribution.—NEW MEXICO. Mesilla Valley (Cockerell, 1899, Fall and Cockerell, 1907), Las Vegas (Fall and Cockerell, 1907). KANSAS. Cove County (Wellman, 1911), Rush County (Williams & Hungerford, 1914), Greeley County (Williams & Hungerford, 1914), Sheridan County (Williams & Hungerford, 1914), Roxbury, McPherson County (Mickel, 1929), Logan County (Mickel, 1929), Ellsworth County (Knaus, 1928), Kiowa County (Knaus, 1928). OKLAHOMA. (Knaus, 1928). TEXAS. (Knaus, 1928). COLORADO. Denver (Schwarz, 1904), Parker (Cockerell, 1905), Colorado Springs (Mickel, 1928), Boulder (Hicks, 1926).

As has been suggested here, there is little basis in the literature for the separation of this species from *mexicana* Dugès, the structural drawings of which are inaccurate and inconsistent in those very characters which have been used to distinguish the two species. In addition, Mickel (1929) has demonstrated that the shape and proportion of the segments of the antennae and palpi are intraspecifically variable. However, in spite of these facts, the tinted plate of the Mexican species published by Dugès (1889*b*) suggests a different insect, and this, coupled with differences in color and distribution, would seem to warrant keeping the two distinct until their status can be determined by direct comparison.

Van Dyke (1928) has shown that *Hornia gigantea* Wellman is the same as *Leonia neomexicana* Cockerell. Mickel (1929) apparently reached the same conclusion independently and also added *Leonidia anthophorae* Mickel to this synonymy. However, I have not seen Cockerell's type, and it has been necessary to accept this synonymy at its face value. Denier (1935), without explanation, recognizes *Leonidia* as a valid genus, *L. anthophorae* as a valid species.

The primary larva of *neomexicana* may be easily recognized by the small number of teeth in the mandibles. In most specimens the number is five but occasionally there may be four or six. From the western form of *minutipennis*, which usually has six mandibular teeth, *neomexicana* may be distinguished by the widely separated processes of the eighth tergite.

Hornia minutipennis Riley

Hornia minutipennis Riley, 1877, Trans. Acad. Sci. St. Louis, 3:564, pl. 5, fig. 13.

Male.—Color of head, thorax, and legs rufous or pale ferrugineous, elytra testaceous, abdomen creamy white with paired, rectangular, dark brown tergal and sternal plates; integument shining, clothed with short, dark brownish hairs. *Head* distinctly wider than pronotum, surface clothed with coarse, erect, dark brown or blackish hairs about as long as

greatest width of antennal segments; punctures large, shallow, close on frons, smaller, sparser on vertex; upper frons slightly concave; antennae eleven-segmented, attaining approximately base of pronotum, first two segments clothed with longer hairs, third segment larger than second; labrum wholly or partially testaceous, sparsely hairy; mandibles dark ferrugineous; maxillary palpi with ultimate segment but little longer than penultimate segment. *Pronotum* nearly as long as broad, subquadrate, basal margin not elevated; surface
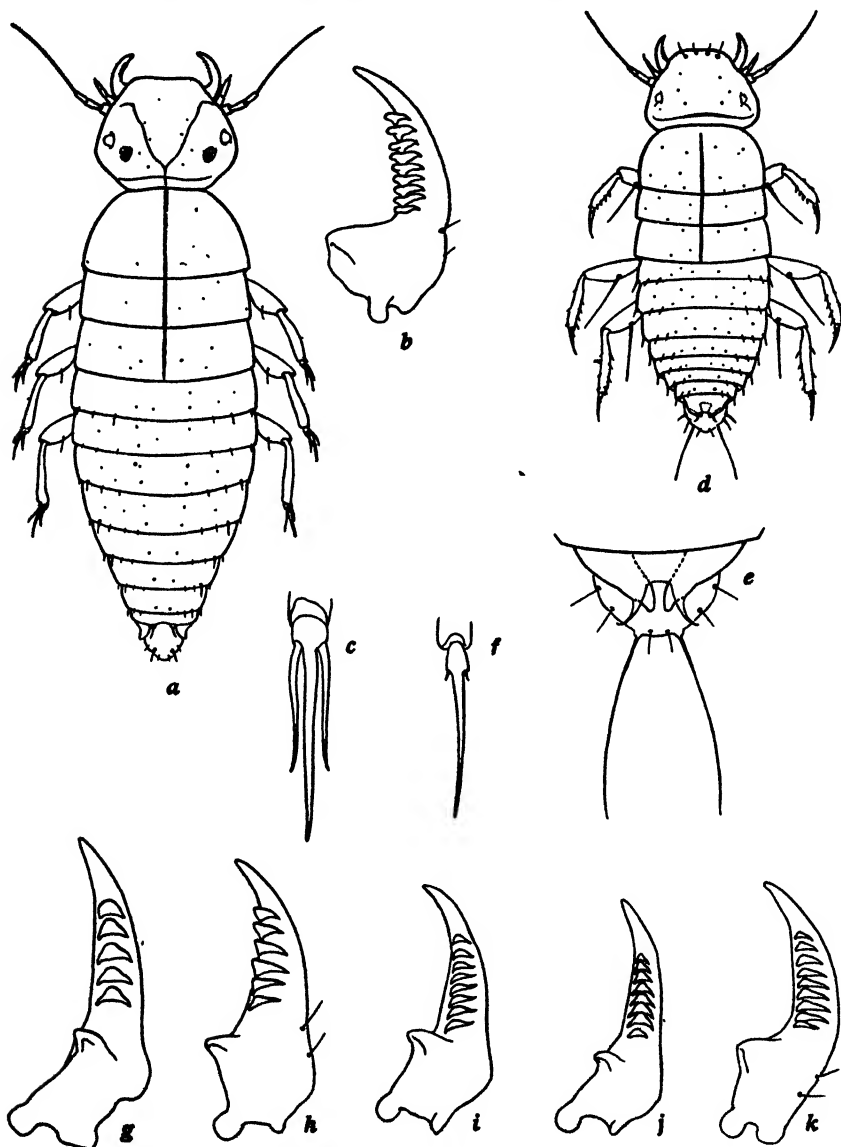
Fig. 1. (*a*) *Hornia boharti* Linsley, primary larva, × 90; (*b*) mandible, × 400; (*c*) intermediate tarsus, × 560; (*d*) *Allendesalazaria nymphoides* Escalera, primary larva, × 90; (*e*) eighth and ninth abdominal tergites, × 300; (*f*) intermediate tarsus, × 560; (*g*) *Hornia neomexicana* (Cockerell), ventral view of right mandible, × 400; (*h*) *Hornia minutipennis occidentalis* Linsley, same, × 400; (*i*) *Hornia minutipennis minutipennis* Riley, same, × 400; (*j*) *Allendesalazaria nymphoides* Escalera, same, × 400; (*k*) *Hornia boharti* Linsley, same, × 400.

irregularly, shallowly punctured, pubescence similar to that of head; scutellum cordiform, a little wider than long. *Legs* clothed with short, coarse, dark brown or blackish hairs about one-half as long as greatest width of tibiae; tarsal claws pale ferrugineous, simple or armed with a short, slender, inner spine which reaches to about middle of claw and is at most only about one-fourth as long as distal claw process. *Elytra* barely extending over basal margin of first abdominal tergite; surface rugose, clothed with coarse black hairs. *Abdomen* large, saclike, elongate oval, twice as long as broad; first tergite feebly sclerotized, lightly pigmented, tergites two to six with paired, rectangular, heavily sclerotized and pigmented plates, seventh and eighth tergites with a single, transverse plate; sternites similarly sclerotized but with the paired plates more widely separated at middle; abdominal pubescence coarse, dark brown or blackish, more or less confined to definite transverse segmental bands. Length 14–16 mm.

Female.—Antennae but little longer than head; abdomen larger, paler, tergal and sternal plates feebly sclerotized, unpigmented or cream color. Length 15–17 mm.

Hornia minutipennis minutipennis Riley
(Figure 3*i*)

> *Hornia minutipennis* Riley, 1877, Trans. Acad. Sci. St. Louis, 3:564, pl. 5, fig. 13; Riley, 1878, Am. Nat., 12:218; Riley, 1878, 1st Rept. U. S. Entom. Com., p. 296, pl. 4, f. 13; Riley, 1879, Can. Entom., 11:30; Beauregard, 1890, Ins. vesic., pp. 407, 454, fig. 144; Cockerell, 1899, Psyche, 8:417; Blatchley, 1910, Coleopt. Indiana, p. 1357; Wellman, 1911, Entom. News, 22:17; Cros, 1913, Bull. Soc. Hist. Nat. Afr. Nord, 4:18; Rau, 1926, Trans. Acad. Sci. St. Louis, 3:236; Mickel, 1929, Entom. News, 40:6; Cros, 1929, Ann. Entom. Soc. France, 98:195; Rau, 1930, Psyche, 37:155.

Adult Male.—Abdominal tergites with sclerotized bands distinct on all segments; tarsal claws simple, without an inner basal tooth.

Adult Female.—Abdominal tergites without sclerotized or heavily pigmented areas; tarsal claws simple.

Primary larva.—Mandibles bearing eight inner teeth; maxillary palpi with ultimate segment distinctly longer than penultimate segment.

Type locality—St. Louis, Missouri.

Hosts.—*Anthophora abrupta* Say (Riley, 1877, as *sponsa* Smith; Rau, 1926, 1930); *Anthophora bomboides* Kby. (R. C. Shannon.)

Recorded distribution.—DISTRICT OF COLUMBIA. Washington (Schwarz, 1904, Cros, 1929). MISSOURI. St. Louis (Riley, 1877), Wickes (Rau, 1926). MONTANA. Helena (Schwarz, 1904).[a]

New record.—NEW YORK. Ithaca (R. C. Shannon).

This subspecies seems confined to the area east of the Rocky Mountains. Accounts of its biology have been given by Riley (1877–79) and Rau (1926, 1930).

Hornia minutipennis occidentalis new subspecies
(Plates 4–5; figure 1*h*)

> *Hornia minutipennis*, Riley, 1899, Proc. Entom. Soc. Wash., 1:147; Schwarz, 1904, Proc. Entom. Soc. Wash., 6:22; Van Dyke, 1928, Univ. Calif. Publ. Entom., 4:402.

Adult male.—Abdominal tergites with sclerotized bands feeble or absent on first two segments; tarsal claws with a distinct inner basal tooth.

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[a] Through the kindness of Dr. E. A. Chapin and Mr. H. S. Barber, I have been able to examine the specimen upon which this record was based. It is in poor condition and may possibly represent a distinct species. However, the claws appear to be simple as in *minutipennis minutipennis*. The example is associated on a pin with *Anthophora* (*Micranthophora*) *peritomae* Ckll.

Adult female.—Abdominal tergites without sclerotized or heavily pigmented areas; tarsal claws with an inner basal tooth.

Primary larva.—Mandibles bearing six, rarely seven, inner teeth; ultimate segment of maxillary palpi scarcely longer than penultimate segment.

Type locality.—Montara, San Mateo County, Calif.

Hosts.—*Anthophora occidentalis* Cresson (Mickel, 1928), *Anthophora stanfordiana* Cockerell (Linsley and MacSwain).

Recorded distribution.—CALIFORNIA. Fresno County (Riley, 1899), Alameda (Schwarz, 1904). COLORADO. Denver (Schwarz, 1904), Colorado Springs (Mickel, 1928).

New records.—CALIFORNIA. Folsom, Sacramento County (Koebele), Pittsburg, Contra Costa County (Linsley and MacSwain), Berkeley (Rivers), 20 miles east of Bakersfield, Kern County (Linsley, MacSwain, G. E. Bohart); San Benito River, 11 miles north of The Pinnacles, San Benito County (Linsley and MacSwain); Livermore, Alameda County (MacSwain).

Types.—Holotype male (Calif. Acad. Sci., Entom., no. 5151), allotype female (no. 5152) and 28 paratypes from Montara, California, May, 1940 (Linsley and MacSwain). Additional paratypes are from the same locality in 1939 and from Pittsburg, Contra Costa County, 1939 and 1940.

This subspecies differs from typical *minutipennis* in the heavier pigmentation of the abdomen and toothed tarsal claws and also in the number of teeth on the mandible of the primary larva. It appears to be confined to the Pacific Coast and Rocky Mountain area and occurs on different host bees. Apparently *occidentalis* is the parent subspecies as it retains the more primitive tarsal structure. This is also borne out by the fact that *occidentalis* occurs in what appears to be the distribution center for the genus *Hornia.*

Hornia boharti new species
(Plates 4–5; figure 1*a, k*)

Adult male.—Color of head, thorax, and legs black, elytra rufous, abdomen creamy white with transverse, dark brown tergal and sternal plates; integument shining, clothed with long, coarse, black hairs. *Head* a little wider than pronotum, surface clothed with coarse, erect, black hairs nearly twice as long as greatest width of antennal segments, punctures shallow, irregularly spaced; antennae eleven-segmented, reaching at least to middle of elytra, third segment a little longer than second, ultimate segment twice as long as penultimate, apex acute; labrum testaceous to black, sparsely clothed with long, coarse hairs; mandibles black; maxillary palpi with last segment but little longer than penultimate segment. *Pronotum* distinctly wider than long; basal margin not elevated; surface shallowly, irregularly, not closely punctured; pubescence long, coarse, black; scutellum cordiform or subtriangular. *Legs* clothed with long, coarse, black hairs as long as, or longer than, greatest width of tibiae; tarsal claws pale ferrugineous, without an inner spine. *Elytra* barely extending across basal margin of first abdominal tergite, surface rugose, clothed with coarse, black hairs. *Abdomen* oval, one and one-third times as long as broad, tergites one to five semi-corneous, each with a large, transverse, sclerotized, black plate, remaining tergites corneous, black; sternites one to six, each with a large, transverse, corneous plate similar to those of tergites, seventh sternite black; abdominal hairs long, coarse, black, numerous, more or less uniformly distributed. Length 7.5–11 mm.

Adult female.—Antennae at most attaining middle of pronotum; abdomen pale, sometimes with poorly defined tergal (but not sternal) plates suggestive of those of male. Length 8–12 mm.

Primary larva.—Mandibles bearing nine (rarely eight or ten) teeth; maxillary palpi with ultimate segment distinctly longer than penultimate segment; eighth abdominal tergite with spiracle-bearing processes separated by more than basal widths.

Holotype male (Calif. Acad. Sci., Entom., no. 5153), allotype female (no. 5154) and 22 paratypes, collected by G. E. Bohart in Grapevine Canyon, ten miles south of Little Lake, Inyo County, California, December, 1939, from nests of *Anthophora linsleyi* Timberlake. Additional paratypes were collected at the same locality April, 1941, by Linsley, MacSwain, and Bohart. Other material, not designated as paratypic, is from 20 miles east of Bakersfield, Kern County, March 31, 1941, in nests of *Anthophora linsleyi* and *A. stanfordiana* Ckll. (Linsley, MacSwain, G. E. Bohart); Blythe, Calif., April 2, 1941, in nests of *Anthophora* n. sp. (Linsley, MacSwain, Bohart); and Pinnacles National Monument, San Benito County, California. An example has also been seen in the collection of Dr. E. C. Van Dyke, taken from nests of *Anthophora linsleyi* in Dowojiby Canyon, near Oilfields, Fresno County, Calif., January 20, 1934, by J. R. Arnold. Paratypes are deposited in the collections of the California Academy of Sciences, the United States National Museum, the University of Kansas, G. E. Bohart, and E. G. Linsley.

Hornia boharti differs at once from the adults the other known American species of the genus by its small size, oval form, very long pubescence, and simple tarsal claws. In appearance it is highly suggestive of *H. neomexicana* (Ckll.) but, in addition to the characters just enumerated, it may be separated by the narrow, short elytra which barely extend across the basal margin of the first abdominal tergite and the feebly sclerotized abdomen in the female. From *H. minutipennis* Riley it may be further distinguished by the elongate antennae which attain the middle of the elytra in the male, the middle of the pronotum in the female, by the robust head and thorax, and by the sclerotization and pigmentation of the abdomen in the male. In the female the abdomen is usually feebly sclerotized and unpigmented as in *minutipennis* but in a few examples the pigmentation of the tergites approaches that of the male. The female illustrated (plates 4–5) is the most fully pigmented in our series. The primary larva has the maximum number of teeth in the mandibles for any member of the genus. The majority of the specimens have nine teeth but examples have been seen with eight and ten.

Genus *Allendesalazaria* Escalera

Allendesalazaria Escalera, 1910, Bol. R. Soc. Espan. Hist. Nat., 10:379; Champion, 1911, Entom. Mo. Mag., 47:16; Champion, 1911, Entom. News, 22:132; Escalera, 1914, Trab. Mus. Nac. Cienc. Nat. Madrid, Ser. Zoöl., 11:380; Parker and Böving, 1924, Proc. U. S. Nat. Mus., 64(23):32.

Adult.—Head about as wide as pronotum, subtriangular, deflexed, suddenly constricted posteriorly, posterior margin straight, neck distinct; clypeus transverse, apex subtruncate; labrum large, transverse, apex feebly emarginate; mandibles prominent, broad at base, outer margin subangularly arcuate, apices slender, acute; maxillary palpi elongate, four-segmented; labial palpi three-segmented; antennae eleven-segmented, segments submoniliform; eyes narrow, transverse, finely facetted. Pronotum wider than long, feebly convex; scutellum transverse; coxae prominent, conical, anterior pair distinctly separated, intermediate pair overlapping posterior pair; legs slender, femora moderately robust, tibiae slender, spurs short, tarsi narrow, claws simple. Elytra greatly abbreviated, squamiform, elongate oval, scarcely surpassing apex of first abdominal tergite; wings rudimentary. Abdomen large, oval, segments corneous; eighth sternite cleft in male, entire in female.

Primary larva.—Head obcordiform, distinctly broader than long, broadly truncate in front, widest behind the middle; epicranial and frontal sutures indistinct; clypeus and labrum fused with frons; labial palpi two-segmented; antennae three-segmented, about as long as head, apical seta long, slender; mandibles multidentate, with seven or eight teeth.

Thorax about as large as abdomen, middorsal suture distinct. Abdomen tapering apically; spiracle of first segment subequal to that of mesothorax, remainder smaller; spiracle bearing processes of eighth tergite longer than basal width, apex subacute; ninth segment with a pair of long caudal setae, longer than the segment, subequal in length with antennal setae. Femoral setae long, coarse; tarsus less than half as long as tibiae, slender, claw-shaped; tarsal setae very short and inconspicuous.

Genotype.—*Allendesalazaria nymphoides* Escalera (monobasic).

Cros (1913, 1920, 1929) has repeatedly regarded this genus as synonymous with *Hornia*. However, the two genera are abundantly distinct in habits and in structure. The adults differ in the shape of the mandibles (evenly rounded in *Hornia*, subangular in *Allendesalazaria*) the form of the scutellum (cordiform in the former, transverse in the latter) and the structure of the abdomen (semimembranous in *Hornia*). The primary larvae of *Allendesalazaria* differ at once in the indistinct frontal and epicranial sutures, long coarse, caudal and femoral setae, and minute lateral processes of the tarsi. The fact that these two wingless genera occur on widely separated continents (Africa and North America) suggests that their resemblance may be superficial rather than the result of close phylogenetic relationship.

Allendesalazaria nymphoides Escalera
(Figures 1*d*, *j*)

Allendesalazaria nymphoides Escalera, 1910, Bol. R. Soc. Espan. Hist. Nat., 10: 380; Champion, 1911, Entom. Mo. Mag., 47: 16, Champion, 1911, Entom. News, 22: 132; Escalera, 1914, Trab. Mus. Nac. Cienc. Nat. Madrid, Ser. Zoöl., 11: 381.
Hornia nymphoides, Cros, 1913, Bull. Soc. Hist. Nat. Afr. Nord, 4: 42; Cros, 1920, Bull. Soc. Nat. Hist. Afr. Nord, 11: 76; Cros, 1929, Ann. Entom. Soc. France, 98: 196.

Adult male.—Color of head, thorax, legs and abdomen yellow-brown or tawny, elytra dark brown; integument shining, clothed with a short, yellowish pilosity. *Head* not wider than the pronotum, vertex smooth with a few moderately deep punctures; antennae eleven-segmented with a tendency for some of the intermediate segments to fuse, attaining the base of the elytra, third segment a little longer than second, last segment longer than penultimate, subacute; mandible with apices piceous; maxillary palpi with ultimate segment oval. *Pronotum* a little wider than long, anterior angles rounded, base truncate, surface finely, inconspicuously punctured; scutellum broad, transverse sublinear. *Legs* smooth; tibial spurs short, obtuse. *Elytra* extending across apical margin of first abdominal tergite, surface strongly rugose, pubescent. *Abdomen* yellow brown. Length 9–10 mm.

. *Adult female.*—Antennae not extending beyond basal margin of pronotum; abdomen pale yellowish brown. Length 9–10 mm.

Primary larva.—Mandibles bearing eight (rarely seven) teeth; spiracle bearing processes of eighth abdominal tergite separated by less than their basal widths.

Type locality.—Mogador, Morocco.

Recorded distribution.—MOROCCO. Mogador (Escalera, 1910), Oudjda (Cros, 1920). ALGERIA. Mascara (Cros, 1913).

Hosts.—*Anthophora* sp. (Escalera, 1910), *Anthophora albigena* Lep. (Cros), *Anthophora talaris*, Perez (Cros, 1913).

Adults and larvae of this species were very kindly made available for study by the authorities of the United States National Museum.

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PLATES

PLATE 5

Hornia boharti Linsley (A) male, (B) female; *Hornia minutipennis occidentalis* Linsley (C) male, (D) female. × 5.

B

D

BIONOMICS OF THE MELOID GENUS HORNIA (COLEOPTERA)

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THE BIOLOGY of the Meloidae has fascinated the entomologist since 1851, when Newport first made known their complex metamorphosis. Through the efforts of Fabre, Riley, Beauregard, Cros, Böving, Milliken, and others, the habits of a number of genera have been disclosed. However, in spite of the work of these men, our knowledge, as measured by the family as a whole, still remains fragmentary. Thus, in 1924, Parker and Böving said that "of 31 North American genera we have complete biological records of only 1 ... and partial records of 2 ... the life history of the remaining 29 being unknown or known only through European publications on European species."

Important contributions toward a knowledge of the life history of *Hornia* have been made by Riley (1877–1879) and Rau (1926–1930). However, conspicuous gaps have remained in our knowledge of both the life cycle and habits of the genus. Such questions as the time, place, and method of mating and the mode of infesting hosts have long remained unanswered. In an attempt to answer these and other questions the authors undertook the present study.

SUMMARY OF LIFE HISTORY

I. *Hornia minutipennis occidentalis* Linsley

Hosts.—*Hornia minutipennis minutipennis* has been recorded from the nests of *Anthophora abrupta* Say (=*sponsa* Smith) in Missouri (Riley, 1877; Rau, 1926) and *H. minutipennis occidentalis* Linsley from *Anthophora occidentalis* Cresson in Colorado (Mickel, 1928, as *minutipennis*). In California, we have thus far found *H. m. occidentalis* only in the nests of *Anthophora stanfordiana* Cockerell. This species of bee occurs most commonly in coastal California and Oregon and is rarely found very far inland. It nests gregariously in vertical or steeply inclined banks and cliffs, most frequently selecting those with a southern exposure. The burrows enter at right angles to the surface and, as is usual in species of *Anthophora,* the entrance is protected by a clay or mud chimney. At a depth of one or two inches the burrows usually incline sharply downward and continue either as a simple or irregularly forked tube, but are subject to modification in different types of soil. Within the burrow a series of three to eight cells, rarely more or less, is arranged end to end. The internal measurement of these cells averages 16 by 10.5 mm. They are constructed individually, waterproofed by a waxlike oral secretion, and provided with pollen, water, and a little honey. The bee then deposits an egg on the food mass and seals the cell with a cap averaging 7.5 mm. in diameter and 3 mm. in thickness. When all of the cells in the series have been provisioned and closed, the burrow is plugged at the ground surface by means of a circular, slightly concave disk of clay or mud. Between this plug and the first larval cell

there remains an air space of variable size. Within two weeks after oviposition the eggs hatch and the young larvae begin to feed on the stored pollen. Their development is very rapid and growth is completed in from three to four weeks. At the conclusion of this feeding period the larva enters a prepupal stage and remains quiescent for from nine to ten months. Under adverse conditions they may remain over until the following year. Pupation follows. Nininger (1920) has assigned seven to eight weeks to the pupal stage, but this was probably because he brought his specimens into the laboratory in the fall. Larvae collected in the field during the spring require a period of only four to

STAGES	HORNIA MINUTIPENNIS OCCIDENTALIS											
	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEP	OCT	NOV	DEC
EGGS				•••••••••	••••••••							
LARVAE				•••••				•••••				
PUPAE								••••••▬▬•••••				
ADULTS				▬•••▬				•••▬				

Legend
▬▬ average duration of stage
••••• total duration of stage

STAGES	ANTHOPHORA STANFORDIANA											
	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEP	OCT	NOV	DEC
EGGS					••••••▬••••••••							
LARVAE					••••••••▬▬••••••••							
PREPUPAE			•••••••••				•••••					
PUPAE			••••▬▬•••••									
ADULTS			••••••▬▬▬▬••••••									
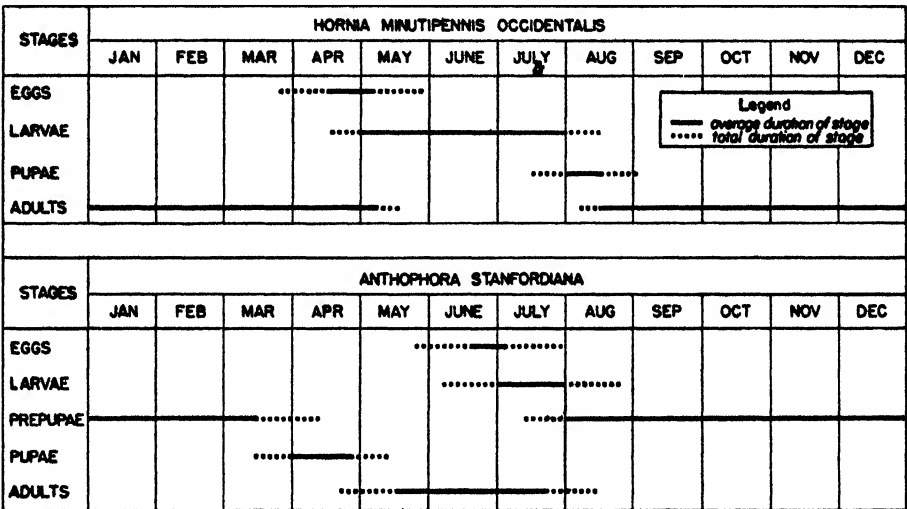
Fig. 1. Comparison of life cycles of *Hornia minutipennis occidentalis* Linsley and its host, *Anthophora stanfordiana* Cockerell.

four and one-half weeks. After transformation, if weather conditions are favorable, the adult remains but a short time in the cell. Emergence is effected by chewing through the cell cap. Ordinarily, bees which are deepest in the cell series must await the emergence of those above. When catastrophe overtakes the individuals nearest the surface, the others are frequently trapped and unable to escape.

In the northern part of its range *Anthophora stanfordiana* is primarily a summer bee. In the central Californian colonies under observation the first adults began to appear early in May and the latest had disappeared by the middle of August. Eggs could be found in the field from the latter part of May until the end of July, and feeding larvae from mid-June to mid-August. The first prepupae were observed early in July, and between the last week of August and the first week of April all larvae removed from their cells were in this stage. Pupae first made their appearance about the middle of April. In the vicinity of Bakersfield, however, the seasonal activities begin four or five weeks earlier.

Localities under Observation.—*Hornia*-infested nesting sites of *Anthophora stanfordiana* were studied in three very different localities in California. The first was in the hot, dry, foothill region three miles south of Pittsburg, Contra Costa County. In this area a small but permanent stream has cut into a hard conglomerate of clay and sandstone, to a depth of about forty feet. For many seasons the steep banks along the north side of this stream have served as nesting grounds for *Anthophora stanfordiana,* and the bank surface is pockmarked with the partly weathered burrows of former years. In the spring these same streambanks are used by *Anthophora edwardsii* Cresson, *Osmia lignaria* Say, and *O. exilis* Sandhouse, and in the summer and early fall by *Sceliphron servillei* (Lepeletier) and *Odynerus* spp. The spring aculeate fauna in this area is supported by extensive fields of *Baeria* and small fields of *Amsinckia* and *Phacelia,* but by the time *stanfordiana* is most active the countryside has begun to dry up and pollen plants are evident only along the stream bottom. In the two seasons under observation these consisted of meager amounts of *Brassica* and *Circium,* providing unfavorable food conditions for the bees. This greatly facilitated the present study, for the bee population was greatly depleted and individual cell series could be isolated for observation. Another important factor that favored the investigation was the hard soil, which was extremely resistant to weathering and which preserved in almost perfect condition the cell series from previous seasons. This made it possible to study the effects of *Hornia* over a period of years and to verify conclusions drawn from observation of the living organisms.

The second locality investigated was at Montara, San Mateo County. In this area *A. stanfordiana* nests in a tightly packed but soft and easily excavated sandy soil near sea cliffs. The sites under observation ranged from cliffs splashed by waves at high tide to banks a hundred yards or more inland. In contrast with conditions in the Pittsburg vicinity, the period of adult activity is characterized by a cool, humid, windy, and commonly foggy weather. The surrounding country supports an abundance of pollen-producing flowers at all times of year, and as a result the area abounds in Aculeate Hymenoptera. Here *stanfordiana* shares the banks, but usually not its restricted nesting sites, with *Anthophora urbana* Cresson, *Gorytes* sp., *Odynerus halophila* Viereck, and at least two species each of *Andrena* and *Colletes*. The stages in the life cycle of both *Anthophora* and *Hornia* at Montara lagged from two to three weeks behind those at Pittsburg.

The third infested area was found along Caliente Creek, 20 miles southeast of Bakersfield, Kern County, California. The bees were nesting in small, scattered groups along a high, clay and sandstone bluff within 75 feet of the stream. Here it was necessary for *A. stanfordiana* to compete for nesting sites with *A. linsleyi,* the dominant species of the area. Among the available flowers, *Lupinus* sp. and *Salvia carduacea* were most abundant, but the pollen source for *stanfordiana* was not definitely determined.

Emergence and Copulation.—*Hornia minutipennis* passes the winter in the bee cell as an adult enclosed in a capsule formed by the exuvia of the fourth

and fifth larval instars. When ready for emergence and mating, the capsule is ruptured by the mandibles or by body movements and gradually worked backward off the body, principally by the legs. Occasionally, however, the adult apparently backs out of its skin case, although this was never actually observed. If the beetle is a female, she ordinarily remains in the cell after cutting a terminal hole a little larger than her head. Before cutting a hole, she moistens the cell wall at the desired point by an oral secretion which seems to soften the surface. The male cuts a similar opening through which, however, he leaves the cell. By means of his mandibles he tunnels slowly along the outside of a cell series until a chamber occupied by a female is encountered. He then enters either through the terminal aperture cut by the female or by means of a similar opening which he bores in the side of the cell. These holes were observed by Rau (1930), who suggested that mating might take place through them, but our observations reveal that the male actually enters the cell for copulation. Thus, normally, neither sex comes to the surface of the ground. An exception may occur when only one sex or one individual is represented in a cell series, but on several occasions we have observed virgin females waiting in the terminal cell long after all the males were dead. Actually, neither sex is well equipped for crawling on a steep bank and both are flightless. The few individuals observed by us on the surface of the ground were males. Another variation in procedure obtains when a female occupies the terminal cell of the series. The female then burrows her way out of the cell and enters the air space below the burrow plug. She then cuts a small round hole in the plug, similar in size and shape to that normally made in the end of her cell, and remains in the chamber until joined either by a male tunneling outward from behind or possibly by an individual wandering on the surface. In both of the colonies studied the sex ratio was one to one.

At the Pittsburg nesting site, the first active adult *Hornia* of the 1939 season was found on April 4. On this date six mature individuals of each sex were observed. Of these, one pair was found in copulation in a cell, four females and three males were in their individual chambers, one male was cutting his way into a female cell, and one was crawling on the surface of the cliff. Similar observations were made on other occasions. In the laboratory it was found that the males will readily enter the small holes cut by the female but that they usually leave after a period of ten or fifteen minutes. When a pair was confined in a glass container, copulation took place intermittently over a period of several hours, and the intervals were utilized by the female for oviposition. When several of each sex were placed together, the same male mated with more than one female, the same female received more than one male. The actual period of copulation is, however, of short duration, varying from five to eight minutes. The male mounts the female immediately after locating her and without the preliminary period of courtship characteristic of other meloids. Also, unlike most other meloids, which copulate in a linear position with the two sexes facing in opposite directions, *Hornia* mates with both individuals facing the same way. This position is always assumed regardless of whether mating

takes place in a bee cell or in an unconfined space. Likewise, the males will continue to copulate until the abdomen is shrivelled and greatly reduced in size. When disturbed, either while mating or when engaged in other activities, the adult *Hornia* readily feign death. The females lived an average of 63 days after mating (minimum 40, maximum 76), and the males 28 days (minimum 25, maximum 32).

Oviposition.—Oviposition begins immediately after copulation. Although most meloids lay their eggs more or less remotely from their host and rely upon the newly hatched larvae to find their own food, the majority of species take some special care with them. Thus *Macrobasis, Epicauta,* and *Poreospasta* prepare special egg cavities in the soil; others, like *Nemognatha, Zonitis,* and *Apalus,* place their eggs on flowers; a few, like *Tricrania,* deposit them beneath loose objects on the surface of the ground. In *Hornia,* however, the female oviposits in the cell in which she developed. This fact was suspected by Rau (1930) and has been confirmed by us. The procedure is modified only by females from the terminal cell, whose eggs are laid in the air pocket behind the burrow plug, or possibly by those few which may find it necessary to emerge in order to mate, such females then re-entering a burrow to lay eggs. The number of ova produced is large and, in the many lots observed by us, the viability was practically 100 per cent. Riley records 680 eggs deposited by a single female of *H. minutipennis minutipennis.* Under laboratory conditions our examples of *occidentalis* averaged 887 eggs with a minimum of 616 and a maximum of 1308. For *Allendesalazaria nymphoides,* Cros reports only 259; Parker and Böving recorded 1925 from a single female of *Tricrania sanguinipennis.* In *H. minutipennis occidentalis* the ovipositing period for an individual lasts about six weeks, after which the female dies. Two-thirds of the eggs are normally laid during the first two weeks of oviposition. At Pittsburg in 1939, oviposition had been completed before the first of May or about two weeks before the earliest *Anthophora* had left their cells. Under laboratory conditions, the average incubation period was 26 days (minimum 24, maximum 28). Unlike *Poreospasta* and many other meloids, the *Hornia* female does not eat her own eggs when confined with them.

Activities of Primary Larva.—The primary larva, when first hatched, is pale yellow, but within two or three hours pigmentation is nearly complete and a dark brown color is assumed. This larva is very active when confined indoors. When footing is insecure it spins a fine, silken thread which issues from the anal opening and is capable of supporting the body. When a group of larvae is confined in a small glass container for 7–10 days, the glass surface is completely covered with this silk. The larvae are also long-lived and, when kept in the laboratory without food, lived for 37–76 days in contrast with those of *Tricrania,* none of which lived more than 11 days (Parker and Böving, 1924), and with *Poreospasta polita* Horn, which we were unable to keep alive for more than 8–10 days.

The primary larvae gain access to the cells of a new brood of bees by one of two methods. Usually they leave their natal cell through the hole cut by the

female parent and make their way to the surface of the ground. Upon the surface of the ground they run about rapidly in the bright sun until able to attach themselves to a bee alighting near them. When a bee or any hairy object passes near, they raise their heads high and spread the mandibles. Even in the absence of this stimulus the same behavior is repeated at intervals. Since *Anthophora stanfordiana* spends a great deal of time alighting on the ground in the nesting area, there is ample opportunity for infection by this method. A second type of infection obtains when the larvae hatch in one of the outer cells of the series. Under such conditions the emerging bees from the cells below must pass through the *Hornia* chamber and a heavy infection results. In the field both sexes of the host were commonly captured bearing larvae. These were attached by the mandibles, usually to the hairs of the thorax or propodeum. No evidence was obtained either in the laboratory or the field, that the larvae ever enter a new cell directly. Once they have reached the surface, there appears to be no tendency to disperse of their own accord or to enter cracks, crevices, or *Anthophora* burrows. Rau (1930) reports the placing of several clusters of primary larvae (of *minutipennis minutipennis*) on a bank in the midst of a colony of *Anthophora abrupta*. These were watched closely for about ten days and showed no signs of dissemination. Eighteen days later the clusters were still intact but reduced in size. A few dead specimens in a nearby spider web suggested to him the possibility that some had been moving about. The inactivity of these larvae was probably due to low temperatures or lack of sunlight, for the larvae we observed in the field dispersed rapidly both by running and by being blown about in the wind suspended on silken threads.

The behavior of the primary larva after it gains access to the cell is fairly characteristic. Its first effort is to locate the egg and when this has been done, it assumes a longitudinal position with the tarsal claws firmly imbedded. The egg is then punctured by the mandibles and the contents almost entirely consumed. This procedure appears to be obligatory and no development of the larva could be induced experimentally with pollen alone. When more than one primary larva gains entrance to the same cell, only one develops. In contrast to *Tricrania,* in which the last larva kills any others present (Parker and Böving, 1924), the first *Hornia* larva to reach the egg is the one that survives and the others die of starvation in the first instar. No cannibalism was witnessed at any time nor was any evidence of this habit observed. Several unsuccessful attempts were made to induce cannibalism by confining larvae together in a bee cell or a small container both in the presence and absence of food (pollen and bee eggs).

Later Larval Development and Pupation.—When the primary larva has once gained access to the egg within the cell, its development is rapid and the remaining larval instars are passed through in a period of about three weeks. When fully fed and ready to moult, the primary larva remains in position on the egg shell and sheds its exuvium, leaving it attached to the shell by means of the imbedded claws. If a portion of the egg content remains after moulting, it

is eaten by the second instar larva before it begins to consume the stored pollen. At the completion of this and the succeeding instar the larva completely frees itself from its old exuvium during moulting. That of the fourth instar, however, is not cast and the larva merely shrinks away from its skin and remains inactive within it. The same is true of the fifth moult, which leaves the larva completely enclosed in a double-walled capsule. The exuvium of the sixth (last) larval instar is ruptured and worked backwards to the posterior

TABLE 1

ASSOCIATED PARASITES, PREDATORS, AND SCAVENGERS IN NESTS OF
ANTHOPHORA STANFORDIANA

Material examined	Pittsburg		Montara		Bakersfield	
	Number of cells	Per cent of total	Number of cells	Per cent of total	Number of cells	Per cent of total
Cells.....................	50	100	250	100.0	100	100
Living *Anthophora*...,......	18	36	98	39.2	70	70
Anthophora killed by mold..	3	6	86	34.4	3	3
Hornia m. occidentalis (Meloidae)..............	15	30	50	20.0	20	20
Hornia boharti (Meloidae) ..					1	1
Lytta incommoda (Meloidae)			6	2.4		
Lytta purpurascens (Meloidae)..............					1	1
Anthrenus verbasci (Dermestidae)...........	5	10				
Melecta californica (Anthophoridae).........	1	2	50	20.0	2	2
Dasymutilla aureola (Mutillidae).............	2	4				
Anthrax sp. nr. *fur* (Bombyliidae)...........	6	12			2	2
Gen. et sp. incert. (Phoridae)					1	1

end of the body, where it remains attached to the ventral surface of the pupa. Pupation occurs in the sac formed by the exuvia of the fourth and fifth larval instars. The pupal period is short, normally of less than two weeks' duration. At Montara most of the larvae pupated about the middle of August and by September 1st they had transformed to the adult stage. The new adults remain enclosed in the larval skin capsule and hibernate in this condition. In the latter part of March or early April activity is resumed, with emergence and mating taking place. There is one generation a year.

General Observations.—Because there is but a single generation each year and the primary larvae hatch at about the time of the emergence of the earliest of their host bees, there is a high percentage of parasitism in the nests provisioned early in the season and negligible parasitism in those constructed later. Thus, in the field, it is usual to find many cell series where the parasitism is high (rarely 100 per cent), others with no parasites at all. The result is that

Hornia alone is never responsible for the extermination of the host colony. Likewise, this close timing saves two associated species of *Anthophora* from parasitism. *Anthophora edwardsii*, which nests in the same banks, is an early spring species and completes its active season before the *Hornia* larvae appear. *A. urbana,* on the other hand, which also uses the same nesting sites, flies too late for parasitism. Under laboratory conditions, however, *Hornia* larvae were reared in the cells of both of these species.

TABLE 2

LONGEVITY OF EMERGED ADULTS

Species and sex	Length of life (in days)																			
	21	24	25	26	27	29	31	32	34	40	63	67	68	69	72	74	76	92	95	103
Hornia m. occidentalis..																				
Male.....			1	2	1	1	1	1												
Female...										1	1	2	1	1	•		1			
Hornia boharti.																				
Male.....	1	1		1					1											
Female...												1				1	1	1	1	1

TABLE 3

INCUBATION PERIOD OF EGGS

Species	Days of incubation											
	23	24	25	26	27	28	40	41	42	43	44	45
Hornia m. occidentalis.........	1	51	62	264	269	120						
Hornia boharti.....							1	6	358	416	266	2

Mold is one of the worst enemies of most bee larvae and death from this source may sometimes account for a 50 per cent loss in the population of *Anthophora stanfordiana. Hornia,* however, suffers very little from mold. When it is most prevalent the beetles are enclosed in the skins of both the fourth and fifth larval instars and are well protected. Thus, although *Hornia* cells are frequently filled with mold, the beetles rarely succumb.

II. *Hornia boharti* Linsley

Host.—Hornia boharti has thus far been found abundantly only in the nests of *Anthophora linsleyi* Timberlake. In one locality an infested cell of *A. stanfordiana* was found where the two species of *Anthophora* shared the same nesting site. *A. linsleyi* occurs in California along the east side of the southern Sierra Nevada, on the Mojave Desert at the base of the San Bernardino Mountains, and in the southern San Joaquin Valley. It nests gregariously, either

in banks or in flat ground, and collects pollen from *Salvia carduacea*. The burrows, unlike those of *A. stanfordiana,* have no trace of a turret or chimney. The cells are similar to, but smaller than those of *A. stanfordiana,* the interior measurement being 10 by 7 mm., and they are usually closer to the surface and less regular in arrangement. In addition, the terminal air space is smaller and may be lacking completely. The burrows are frequently borrowed by *Anthocopa xerophila* (Ckll.) but none of the cells of this bee were found to be infested with *Hornia*.

Localities under Observation.—*Hornia boharti* was discovered by G. E. Bohart in a colony of *Anthophora linsleyi* in Grapevine Canyon, 10 miles south of Little Lake, Inyo County, California, in December, 1939. The *Anthophora* were nesting in a vertical bank of hard conglomerate soil. The nesting site extended along the bank for 25 or 30 feet. From this site a section with two square feet of surface area was removed and transferred to the laboratory. Subsequent examination revealed that this small block contained more than 700 cells of *Anthophora linsleyi,* of which about 40 were infested with *Hornia*. In the spring of 1941 the writers visited the locality and collected an additional 1470 cells of which 376 contained *Hornia* in various stages.

A second *Hornia*-infested nesting site of *Anthophora* was found by us along Caliente Creek, 20 miles southeast of Bakersfield, Kern County, California. In this area *Anthophora linsleyi* and *A. stanfordiana* were nesting along a high clay and sandstone bluff. The populations of the former species were distributed in a number of dense, separate colonies, the latter in small, scattered, separate groups. *Hornia boharti* was found in 14.6 per cent of the cells of *A. linsleyi,* in only 1 per cent of the cells of *A. stanfordiana*. This was the only locality encountered in which both species of *Hornia* and both species of *Anthophora* were taken.

Emergence and Copulation.—Unlike *Hornia minutipennis,* which has a one-year life cycle, *H. boharti* requires two seasons to complete its development, spending the first winter and most of the following year as a fifth-instar larva enclosed in a capsule formed by the exuvium of the fourth instar. In the autumn of the second year the larva goes rapidly through a fifth instar, pupates, then transforms to an adult. The adult passes the second winter in a capsule formed by the exuvia of the fourth and fifth instars. Emergence occurs in the very early spring, and the nesting site is fully infested with larvae by March, when the first *Anthophora* appear. In the laboratory, emergence of the adults took place and all individuals were sexually mature in January. *H. m. minutipennis* is not sexually mature until late February or early March. Adults were much more active than those of *minutipennis* and moved about with less difficulty. Mating and sexual behavior were similar to that of the other species. The females lived an average of 82 days after mating (minimum 67, maximum 103), and the males 26 days (minimum 21, maximum 34).

Oviposition.—After mating, the female oviposits in her natal cell. The two-month ovipositing period is two weeks longer than in *minutipennis,* and the average number of eggs is lower (549 as compared with 842). Under labora-

tory conditions the incubation period was 43 days in *boharti* and only 26 days in *minutipennis*. Virgin females began to oviposit 28–44 days after emergence, but laid less than half as many eggs (188–200), which soon collapsed and dried up. Unmated females lived as long as mated females (72–95 days).

TABLE 4

Associated Parasites, Predators, and Scavengers in Nests of
Anthophora linsleyi

Material examined	Little Lake		Bakersfield	
	Number of cells	Per cent of total	Number of cells	Per cent of total
Cells examined.....................	1920	100.00	759	100.00
Living *Anthophora*................	909	47.34	370	48.75
Anthophora killed by mold.........	203	10.58		
Hornia boharti (Meloidae).........	458	23.85	111	14.62
Trogoderma ajax (Dermestidae)....	118	6.14	40	5.27
Melecta californica (Anthophoridae)	75	3 91	44	5.79
Nemognatha apicalis (Meloidae)....	6	.31	44	5.79
Anthrax sp. nr. *fur* (Bombyliidae)..	76	3.96	33	4.34
Photopsis spp. (Mutillidae)........	42	2.19	20	2.63
Hylemya cilicrura (Anthomyiidae)..	20	1.04		
Ptinus californicus (Ptinidae)......			32	4.21
Lytta purpurascens (Meloidae).....			29	3.82
Lytta occipitalis (Meloidae)........			11	1.45
Lytta chloris (Meloidae)..........			7	.92
Monodontomerus montivagus (Callimomidae).................	5	26	4	.52
Triepeolus mojavensis (Nomadidae)			3	.39
Chrysis (*Chrysis*) sp. (Chrysididae)			3	.39
Chrysis sp. (Chrysididae)..........			3	.39
Plodia interpunctella (Pyralidae)...			3	.39
Tineola biselliella (Tineidae).......			2	.26
Oryzaephilus surinamensis (Cucujidae).....................	5	.26		
Gen. et sp. incert. (Ichneumonidae) .	2	.10		
Sitodrepa panicea (Anobiidae)......	1	.05		

Activities of Primary Larvae.—The primary larvae appear early in March, a month in advance of those of *occidentalis.* Upon hatching they make their way to the surface of the ground and there await their host. The pattern of surface activity is similar to that of *occidentalis*, but in *boharti* the female host bee (*Anthophora linsleyi*) is more active in the nesting area than the male and becomes much more heavily infested with larvae. Thus a single female, captured at Pinnacles National Monument while visiting flowers of *Oenothera*, carried 36 primary larvae. When deprived of food, the primary larvae of *boharti* lived only 21–42 days as compared with 38–76 in *occidentalis.* When confined together, or with larvae of *occidentalis*, they showed no evidence of cannibalism.

CONCLUSIONS

In California, *Hornia boharti* and *H. minutipennis occidentalis* are normally parasitic in the nests of *Anthophora linsleyi* and *A. stanfordiana* respectively. The activities of both species are closely timed with those of their hosts and other associated bees that use the same nesting sites are not parasitized. The two species of *Hornia* differ in length of life cycle, time of sexual maturity, length of oviposition period, number of eggs produced, longevity of both primary larvae and adults, place of mating, and in walking and climbing ability of the adults. They differ from all other meloids whose habits are known in that mating and oviposition take place in the natal cell of the female and neither sex normally comes to the surface of the ground. Both species depend upon the activities of the primary larvae to provide access to a new host. The larvae normally wait on the surface of the nesting site until a bee approaches near enough to permit attachment. When access to a new cell has been achieved, feeding upon the bee egg is obligatory to further development. This is followed by the usual series of changes characteristic for the subfamily Nemognathinae. Hibernation is accomplished by the adult in a capsule formed by the exuvia of the fourth and fifth instar larva.

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PLATES

THE INTERNAL ANATOMY OF
DERMACENTOR ANDERSONI STILES

BY

J. R. DOUGLAS

CONTENTS

THE INTERNAL ANATOMY OF DERMACENTOR ANDERSONI STILES

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INTRODUCTION

IN THE PAST half century there has been an ever-increasing interest in the Ixodidae as a result of their incrimination in the transmission of disease. Perhaps the most important member of the group in this respect is *Dermacentor andersoni* Stiles, 1908, which is known to transmit Rocky Mountain spotted fever, tularaemia, and Colorado tick fever, and to produce tick paralysis. There have also been isolated from this tick a number of bacteria and filterable agents the disease relationships of which have not been determined.

In the light of these findings, one would expect every effort to be made to investigate each avenue which might conceivably shed some light on the activities of this tick. This has been done, with one exception. While extensive investigations have been made on the ecology, relationship to disease transmission, and external anatomy for taxonomic studies, practically nothing has been known, or at least published, on the internal anatomy of *D. andersoni*, or, for that matter, any member of the genus *Dermacentor*.

It is not my contention that a knowledge of the internal anatomy will necessarily solve or even assist in the solution of problems concerning *D. andersoni* and related species, but at least it will eliminate certain unknowns and contribute to a fuller understanding of the whole problem of disease transmission by Arthropods.

The first general work on the internal anatomy of a tick was that of Pagenstecher (1861) on *Ixodes*. Nordenskiöld (1905, 1906, 1908, 1909, 1911) and Samson (1909) also contributed to the knowledge of this genus. Robinson and Davidson (1913) published what is probably the best work to date on *Argas*. Allen (1905) and Williams (1905) published rather fragmentary papers on *Boophilus*. Christophers (1906) described briefly the internal anatomy of *Ornithodoros* and *Hyalomma*, and Bonnet (1907) attempted to cover the Ixodidae as a whole, with very few references to *Dermacentor*. In addition to these general works there are many others dealing with one or two phases of the internal anatomy of various species; these will be referred to in subsequent parts of the text. For a complete bibliography of the Ixodoidea up to 1915 the classic works of Nuttall, Warburton, Cooper, and Robinson (1911, 1915) should be consulted.

Histologically there is a fundamental similarity throughout the Ixodoidea, as one would expect. Major differences are morphological rather than histological. In view of this fact, the emphasis in the present work has been placed on morphology except where the structure under consideration differed from descriptions by other workers.

A prime requisite of any anatomical investigation is a set of "labels" which are in common use and have the same meaning when applied to other members of a group. Unfortunately, this ideal has not yet evolved with respect to the Ixodoidea. Many authors have named structures without regard for previous work, and sometimes the name was based on a supposition with respect to function which proved to be erroneous. In this investigation the author has adhered as closely as possible to the terminology of Robinson and Davidson (1913), which on the whole is excellent, in the belief that it will be an additional step toward a standard terminology.

MATERIALS AND METHODS

The specimens used in this investigation were supplied through the kindness of Dr. R. R. Parker, Director of the Rocky Mountain Laboratory, United States Public Health Service.

Numerous gross dissections of *D. andersoni* were made in order that the relationship of the various organs and systems might be thoroughly understood and the microtome sections properly interpreted. The ticks were placed in a small petri dish partly filled with paraffine, and a small amount of paraffine was melted around the specimen, imbedding the legs; for ventral dissections, the material was built up slightly around the margin of the body. The specimen was next flooded with normal saline, tap water, or, if parts were to be removed for subsequent sectioning, a fixative such as aqueous Bouin's or Kahle's. By means of razor-blade scalpels fixed on the ends of short lengths of glass tubing, an incision, commencing at the scapula, was made around the margin of the body. The intestinal diverticulae are not ruptured by this method, when it is used with care, unless the tick is considerably engorged. By the use of finely ground forceps the integument was reflected toward the anterior end while the adherent muscles, tracheae, and so on, were gently separated by blunt dissection. The preparation was then ready for any desired operation.

In order to observe many of the finer details I sometimes found it necessary to stain the dissection; tincture of iodine, malachite green, picric acid, methylene blue, and haematoxylin served this purpose very well. It should be borne in mind, however, that material so stained may be rendered worthless for histological purposes.

The preparation of sections of ticks for microscopic observations presents several difficulties. The integument is so tough, or may become so brittle in the course of preparation with the usual alcohols, that it is impossible to obtain satisfactory sections. Furthermore, the integument is practically impermeable to most fixatives.

Four procedures circumvented these difficulties, with varying degrees of success:

1) Small incisions were made on the periphery of a living tick, which was then fixed in Carnoy-Lebrun, strong formula, and run through graded alcohols to 56° C. paraffine and imbedded in the usual manner. This method, while giving excellent fixation, hardened the integument so that it was extremely difficult to section.

2) Specimens fixed as in the first method were double-imbedded in paraffine and celloidin, the method of McIndoo (cited in Lee, 1928) being used. This usually gave good results, but was somewhat slow, requiring from nine to twelve weeks for penetration of the celloidin.

3) Specimens were dissected as in making gross dissections; Kahle's fixative was used as the dissecting fluid. The dorsal integument was removed and the complete viscera were dissected away from the ventral surface; the capitulum was left attached, to facilitate handling with forceps, and was imbedded in 56° C. paraffine in the usual manner. Although the various organs become quite distorted, this method is excellent for the study of histological detail.

4) Minute incisions were made at several points around the margin of the body, and the modified procedure of McClung (1936) was employed as follows. The specimens were: (*a*) fixed in mixture of one part Dioxan[1] with two parts picro-formol-acetic solution (Bouin's etc.); (*b*) washed in Dioxan; (*c*) dehydrated and cleared in fresh Dioxan; (*d*) infiltrated with warm mixtures of paraffine and Dioxan with increasing proportions of paraffine; (*e*) infiltrated in paraffine; (*f*) sections were cut, spread, and dried; (*g*) decerated in xylol or Dioxan; (*h*) stained (the alum-

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[1] Dioxan is the common name for diethylene oxide.

haematoxylin method of Galigher (1934) was employed, eosin being used as a counterstain) ; (*i*) washed; (*j*) dehydrated in graded alcohols; (*k*) treated with xylol; and (*l*) mounted in Canada balsam or Euparal. (Euparal "Vert" gave good contrast with haematoxylin stains).

The McClung procedure gave excellent results. The Dioxan prevented excessive hardening of the material, rendering it quite easy to section. Moreover, the method requires a minimum number of reagents and is quite flexible so far as the time in the various mixtures is concerned.

The observations reported in the present paper were limited to ticks which had become adult but which had not engorged or been fertilized. Many specimens were allowed to feed from three to five days in order that certain anatomical details might be more easily discerned.

EXTERNAL ANATOMY

The taxonomy of *D. andersoni* has been studied rather intensively; consequently the general external characters are well known and I can add nothing concerning them. Therefore the following section is confined to a discussion of the integument and mouthparts. Other cutaneous structures, such as the anus, genital orifice, Haller's organ, eyes, dorsal fovae, and porose areas, will be described in subsequent sections dealing with the organ systems to which these structures are related.

INTEGUMENT
(Fig. 1; pl. 20)

Morphologically the integument differs markedly in the sexes. The integument of the male is very rigid as compared with that of the female, the only elastic areas being those on the ventral surface, on the lateral margins, and between the large coxae

(pl. 9, *B*). The entire dorsal surface of the male is covered by the scutum, which is heavily sclerotized. The female integument, however, is for the most part elastic, with the exception of the scutum, which is much smaller than that of the male (pl. 8). The reason for the elasticity of the female integument becomes immediately evident upon microscopic examination. Sections through the integument (pl. 20, *E*) show that, excluding the hypodermis, it is composed of two layers: a thin inelastic but pliable external layer which is thrown into a series of folds, and thick elastic internal layer. As the female engorges, these folds become flattened until they disappear when the limit of engorgement is reached.

The integument of both sexes bears numerous pores, pits, and hairs, most of which are considered to be sensory in function and as such are described in another section. There are, however, structures which have no evident sensory connections and are quite similar in appearance to the

Fig. 1. Schematic longitudinal section through an "integumentary gland."

hypodermal glands of *Ixodes* as described by Nordenskiöld (1911). Although they are found in both sexes, they are more or less confined to the elastic ventral portions of the integument in the male. In the female they are much more numerous and are found distributed over most of the integument.
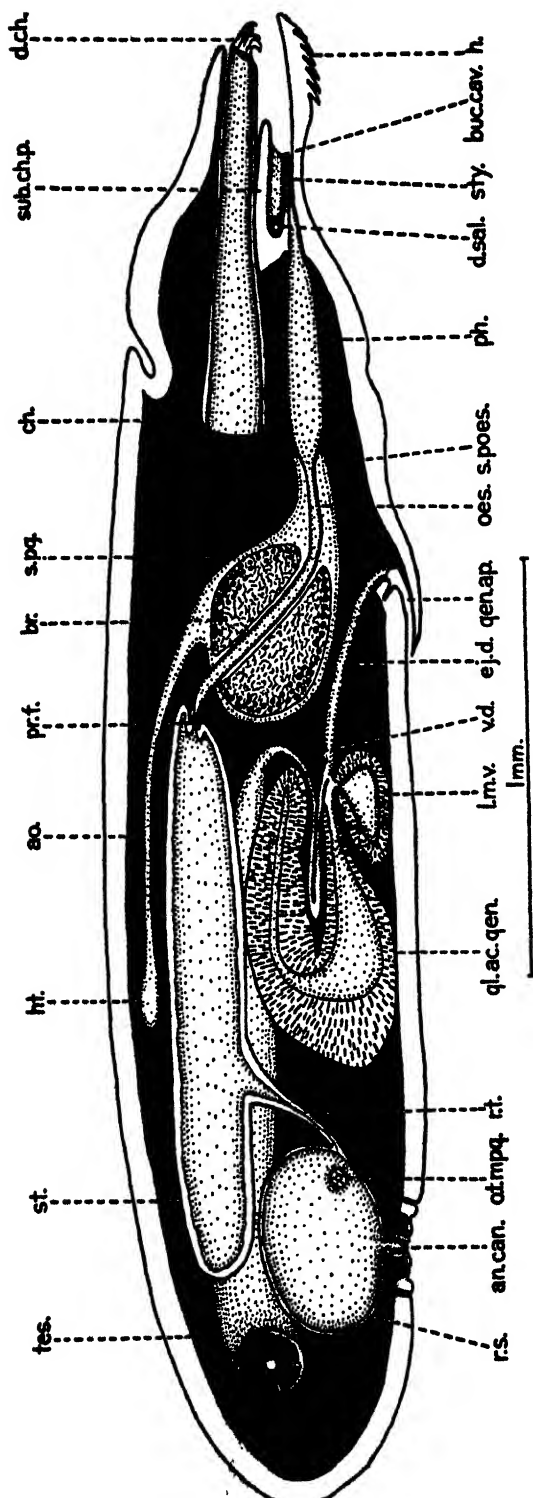
Fig. 2. Schematic view of the left side of the body of a male, showing the relationship of the principal organs.

(See pp. 231–232 for explanation of abbreviations used.)

In section (fig. 1) it is seen that these so-called hypodermal or integumentary glands consist of a pore with a basal modified hypodermal cell which sends a protoplasmic process into the pore for over one-half its length. At its termination in the pore the cellular process connects with a chitinous tubelike structure which is produced from the wall of the pore as shown in figure 1. Similar structures have been called hypodermal glands or integumentary glands in other species of the Ixodidae, but this is purely speculative and does not appear to be justified morphologically. Notwithstanding the fact that sensory connections were not evident, these structures appear to be more closely related to the chemoreceptor type than to the secretory type.

MOUTHPARTS
(Fig. 3; pls. 10, 11, 22)

The mouthparts, along with their basal structures, may be more correctly termed the capitulum. This structure is in the camerostome between the scapulae on the anterior margin of the body and is articulated with the body through the camerostomal fold (pl. 8, *A*, cam. f.). The capitulum consists of four primary structures: the basis capituli (b. c.), the palpi (p.), the hypostome (h.), and the chelicerae (ch.).

The basis capituli (pl. 22) in dorsal view appears as a roughly rectangular, heavily sclerotized structure; in the female it bears a pair of sensory structures, the porose areas (pl. 8, *A*, por. ar.), which will be discussed more fully in the section dealing with special sense organs. In transverse section (pl. 10) the basis capituli appears as a rectangular ring, forming the capitular foramen, the "mouth ring" of Allen (1905) and other authors, through which pass the shafts of the chelicerae, the pharynx, the capitular nerves, and the muscles of the capitulum. The capitulum is capable of moving only in the vertical plane and is actuated by two sets of antagonistic muscles (fig. 3). The levator muscles (m. l. c.) are inserted on the posterodorsal margin of the basis capituli and originate in two groups on the anterior portion of the ventral surface of the cervical grooves (fig. 7). The depressor muscles of the capitulum (m. d. c.) originate on the posteroventral margin of the basis capituli and are inserted in two groups on the posteroventral arms of the cervical grooves.

The palpi are attached to the anterolateral surface of the basis capituli and are made up of four articles. The first articulates freely in a horizontal plane with the basis capituli, whereas articles II and III are rigidly fused. The palpi articulate by means of an antagonistic pair of muscles inserted on the basis capituli and similar to those found in the legs. Article IV (pl. 10, *A*) is greatly reduced in size and is inserted into the end of article III. It is primarily a sensory structure, being thickly covered with sensory hairs. The lateral margins of the palpi are convex in outline, whereas the mesial surfaces are concave so as to fit closely around the hypostome and chelicerae. In ventral view it is seen that the mesial margins of the palpi are studded with large spines which interlock under the hypostome.

The hypostome is an unpaired prolongation of the anteroventral portion of the basis capituli. In ventral view it appears somewhat club-shaped, with the narrow necklike portion merging with the basis capituli. Its ventral surface bears approximately 55 recurved teeth arranged in six rows. The distal end of the hypostome bears a large number of very small, sharp, recurved teeth (pl. 20, *D*). In transverse section the hypostome appears somewhat crescentic in the distal portion, becoming nearly semicircular toward the proximal end. As it fuses with the ventral wall of the capitular foramen, the hypostome becomes expanded into a rectangular structure which forms the subcheliceral plate (fig. 2; pl. 10, sub. ch. p.), supporting the

chelicerae and containing the buccal cavity (buc. cav.) and oral stylet (sty.). On its dorsal surface the hypostome is grooved to form the hypostomal gutter (h. g.). This gutter becomes progressively larger toward its proximal end, where it contains the oral stylet. As the oral stylet is an integral part of the digestive system, it will be described more completely in another section.

The hypostome functions as an anchor holding the mouthparts in place during feeding. The very small teeth on the tip serve as a means of introduction, while the larger teeth hold fast once the hypostome is inserted.

The chelicerae (fig. 3; pls. 10, 11) are heavily sclerotized, paired tubular structures about 1 mm. in length, extending from near the tip of the hypostome posteriorly through the capitular foramen into the body cavity. Near the anterior end
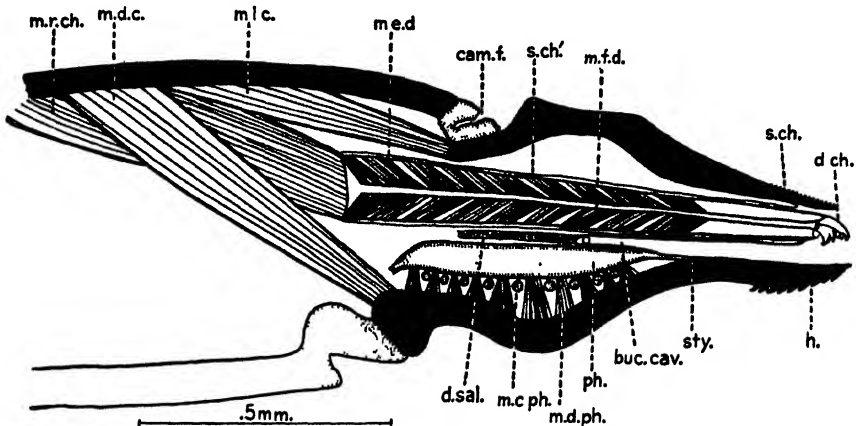
Fig. 3. Schematic longitudinal section through the anterior portion of the body, showing the disposition of the capitular muscles. (See pp. 231–232 for explanation of abbreviations used.)

they are nearly circular in outline, becoming expanded and somewhat oval in shape at the posterior end. Throughout their length the opposing surfaces are slightly flattened, which permits them to lie very close together and prevents any rotation within the sheath. The chelicerae are actuated by powerful retractor muscles (m. r. ch.), inserted on their posterior ends and originating on the ventral surface of the scutum between the posterior arms of the cervical grooves (fig. 7). Concerning the chelicerae, Matheson (1932, p. 32) writes: "The proximal part is dilated and to it are attached the extensor and retractor muscles of the mandible." I have been unable to find any extensor muscles attached to the chelicerae, however, and conclude that they are extended in some other manner, perhaps by the cutting and burrowing action of the sharp digits.

At the anterior end the chelicerae bear a set of ventrally directed toothed digits adapted for piercing flesh. These consist of an internal article (i. a.) and an external article (e. a.). The former bears a toothed dorsal process (d. p.) and the latter bears two large teeth and articulates on the base of the internal article. These digits rest on a shelflike projection of the inner surface of the cheliceral wall and are actuated by two sets of muscles, the flexors and extensors (m. e. d., m. f. d.), which are attached to the basal portion of the digit through a pair of tendons (t. f. d., t. e. d.) and have their origin in the wall of the cheliceral shaft.

The chelicerae are invested on the dorsal surface by a projection of the midportion of the dorsal wall of the basis capituli, and form the external cheliceral

sheath (s. ch.), which bears minute denticles over most of its dorsal surface. This sheath is reflected back ventrally so that it surrounds each of the shafts of the chelicerae and is attached to them at or near their posterior ends, forming the internal cheliceral sheaths (s. ch.') in which the chelicerae slide.

DIGESTIVE SYSTEM
(Fig. 4; pls. 12, 13, 14, 23)

The organs of digestion and excretion constitute by far the largest organ system of the body and present the greatest histological diversity. These organs may be divided into three easily recognizable groups: the foregut, midgut, and hindgut.

FOREGUT

The foregut will be considered here as that portion of the alimentary canal, with its appendages, which extends from the orifice of the oral stylet to the stomach or ventriculus. It is composed of the following parts: the buccal cavity, oral stylet, pharynx, oesophagus, and the salivary ducts and glands.

The buccal cavity (buc. cav.) is an undifferentiated cavity formed in the subcheliceral plate above the oral stylet. Its chitinous lining is continuous with the wall of the oral stylet. In dorsal outline it appears somewhat semicircular with the salivary ducts opening into its posterolateral angles. In transverse section it appears as a broad, flattened tube with its floor resting on the dorsal surface of the posterior prolongation of the hypostomal gutter, forming an enclosed passage in which the oral stylet lies.

The oral stylet (pl. 12, sty.) was first described by Sen (1934, 1935) in *Ornithodoros* and *Amblyomma*. He described and figured it as a rather long, thin, chitinous, tubular prolongation of the pharynx. I found essentially the same structure. In *D. andersoni*, however, the stylet is tripartite and quite short, extending only about one-third the length of the hypostome. The exact manner

Fig. 4. Schematic views of the pharyngeal valve. *A*, Transverse section as it appears when open. *B*, Transverse section as it appears when closed. *C*, Dorsal view. (See pp. 231–232 for explanation of abbreviations used.)

in which ticks feed has long been a matter of speculation, but with the discovery of the oral stylet the true mouth of ticks appears to be found and their feeding mechanism can be readily understood.

The pharynx (ph.) is the powerful sucking structure of the alimentary canal. Approximately 0.5 mm. in length, it lies in the median line, ventral to the chelicerae and beginning at a point about one-third the length of the chelicerae posterior to the tip. It is fusiform in shape. At its anterior end, where it joins the oral stylet, is found the pharyngeal valve (fig. 4), a structure which prevents regurgitation when the pharynx is contracted.

In dorsal view the pharyngeal valve appears to consist of two curved posterolaterally directed alae (a. ph. v.), which are actually projections of the chitinous foregut wall. In transverse section it is seen that these alae are concave dorsally and possess a number of muscle bundles (m. c. ph. v.) which originate on the dorsal

surface of the alae and are inserted on the dorsal wall of the pharyngeal valve. On the ventral surface of the dorsal wall is a toothlike projection which aids in closing the passage. When the constrictor muscles contract, the alae bend and cause the flexible ventral portion of the passage to pinch together. When the muscular tension is relaxed the inherent resiliency of the alae serves to reopen the passage.

In transverse section (pl. 13, *A*) it is noted that the pharynx consists of six heavily sclerotized plates connected by a flexible membrane and arranged in the form of two Y's placed with their bases together. The sides are formed by a pair of large concave plates and the dorsal and ventral surfaces by two pairs of smaller plates.

The action of the pharynx is controlled by three sets of muscles (fig. 3), the lateral and ventral dilator muscles (m. d. ph.) and the circumpharyngeal constrictor muscles (m. c. ph.). The paired lateral dilators are the largest and have their origin in the lateral walls of the basis capituli and their insertion on the lateral pharyngeal plates. The ventral dilators originate in two groups on the floor of the basis capituli and are inserted on the ventral plates of the pharynx. The constrictor muscles are four in number and are arranged so that they connect the arms of the pharynx.

The oesophagus (oes.) is a simple channel connecting the pharynx and stomach. Leaving the pharynx, it approaches the brain, curves sharply downward, and enters the ventral surface of the brain at a point about one-third the distance toward its posterior end. Entering the brain, the oesophagus curves upward at approximately a 45° angle and emerges at a point about two-thirds the distance toward the posterior end. Its course then flattens somewhat and it enters the stomach, forming the proventricular fold.

In transverse section (pl. 13, *C*) the oesophagus is seen to consist of large irregularly angular cells, with indistinct cell walls, resting on a thin basement membrane. The nuclei are quite large, irregular in shape, and tend to be situated toward the base of the cells. Over the irregular projection of cells into the lumen is an extremely thin chitinous layer, continuous with the pharyngeal plates.

At its termination in the stomach the oesophagus forms the proventricular fold (pl. 13, *B*), a structure designed to prevent the flow of blood from the stomach into the oesophagus. As the oesophagus projects into the stomach its cells tend to become cuboidal and their nuclei become regularly spherical. As these cells recurve to meet the cells of the stomach they gradually merge into the characteristic form found in the stomach. The proventricular fold is regulated by a circular constrictor muscle (m. c. prov.) situated in that part of the fold which projects into the stomach.

The salivary glands (pl. 23, gl. sal.) appear as two large, elongate grapelike clusters of spherical alveoli lying along the lateral portions of the body cavity and extending from near the scapulae to a point over the stigmal plates. Their secretion empties into the buccal cavity through large, paired chitinous ducts (d. sal.) very similar in structure to the tracheae. The mass of each gland consists of nearly spherical alveoli approximately 0.04 mm. in diameter. Careful observation reveals the presence of two types of alveoli. The first type (pl. 14, *D*), which constitutes most of the gland, is the granule-secreting alveoli (g. s. a.) and consists of about fifteen large cells arranged around a small central lumen which communicates with a small efferent duct. The cells of an alveolus of this type may be seen in practically any stage of secretory activity, from that in which they are gorged with ferment granules and secretion to that in which they appear as pale reticulated cells devoid of granules. The cells filled with secretory products stain intensely with eosin, whereas those which have given up their secretory products take the eosin very lightly. The nuclei of the granule-secreting alveoli are very large, deep-staining, and tend to become situated near the base of the cell.

The alveoli of the second type (pl. 14, *C*) were first described in detail by Bonnet (1906), who thought they were venom glands. Nordenskiöld (1908) indicated the two types of alveoli in his figures, but failed to describe them. A short while later, Samson (1909) described and figured both types, giving to the alveoli of the second type the name *Pyramidenzellen*. These are markedly different from alveoli of the first type. Their location in the gland is restricted to the anterior third, where they are found closely connected to the salivary duct by means of short efferent ducts, and usually cover most of the lateral and dorsal surfaces. Histologically they are identical with the alveoli described in *Argus persicus* by Robinson and Davidson (1913), consisting of an indefinite peripheral cellular structure with numerous fibrils radiating toward the lumen and apparently ending free. The nuclei are very small and few in number and usually appear to be in the lumen, in contrast to the granule-secreting alveoli, in which the nuclei are basal.

The salivary alveoli empty into a central duct, either by means of direct efferent ducts or secondary and even tertiary ducts. The main salivary duct emerges free from the gland just before it enters the capitular foramen, where it empties into the buccal cavity.

Inasmuch as I conducted no experimental work, I shall not enter into a discussion of the function of the two types of salivary glands. There is probably no doubt, however, that an anticoagulant principle is elaborated. For a discussion of the function of the salivary glands in other species, the reader is referred to the papers by Sabbatani (1899), Nuttall and Strickland (1908), Nuttall (1909), Elmassian (1910), Ross (1926), Pavlovsky and Chodukin (1929), Von Künnsberg (1911), and Jucci (1927).

MIDGUT
(Fig. 2; pls. 13, 14, 23)

For the purposes of this discussion, the midgut will be considered as that part of the alimentary canal which lies between the oesophagus and the rectum. It is composed of the stomach, alimentary caeca, and rectal tube. The Malpighian tubules will be considered in conjunction with the hindgut.

The stomach (st.), with its caeca (fig. 2; pl. 14, *E*), is the largest and most striking organ of the body. Upon dissecting away the dorsal body wall, one is confronted by a maze of large, black, irregularly tubular structures covering most of the viscera.

At its anterior end the stomach branches into two large lateral lobes. These, in turn, branch into anterior and posterior lobes. The anterior lobe divides into two short caeca, which terminate near the anterior margin of the body. The posterior lobe gives off laterally a short lobe which extends under the viscera, ending blindly. The posterior lobe continues caudad and divides into a long lateral lobe which recurves under the viscera, ending in the mid-portion of the body, and a shorter median lobe which curves under the viscera, running in a median cephalad direction.

At its caudal end, in the posterior third of the body, the stomach gives rise to two pairs of caeca arranged somewhat in the same manner as the tines of a fork. These lobes extend to the caudal margin of the viscera, curve under it, and proceed a short distance cephalad.

In the floor of the stomach, near its caudal end, is the orifice of the rectal tube (r. t.), a short funnel-shaped structure which opens into the anteroventral aspect of the rectal sac (fig. 2).

Basically the stomach and caeca are identical in structure. Both vary histologically, however, depending upon the state of digestion. The cells of the stomach and caeca (pl. 13, *D*) are extremely irregular; they may be cuboidal, pyramidal, or clavate. They almost always contain black granules ranged along the cell wall, giv-

ing a vacuolate appearance. The nuclei are spherical, quite large, and usually central in location. For a discussion of digestion in the Ixodidae I would refer the reader to the work of Roesler (1932), Nordenskiöld (1905), and Samson (1909).

The cells of the rectal tube, where it joins the stomach, are quite like those of the stomach proper, but as the rectal end is approached, the cells become more and more compressed, and the lumen becomes progressively smaller until it apparently disappears a short distance before the rectal sac is reached (pl. 13, *E*, *F*). However, there is little doubt that patency may be established since the feces of greatly engorged ticks are often found to contain black debris from the gut. It is quite likely that the rectal tube is closed most of the time, the Malpighian tubules providing the only means of excretion. Blanc (1910) considered this problem and concluded that the varying results of other workers were due to the different species employed. He further states that the *tube communicatif* is always open in the Argasidae but may be closed physiologically, if not anatomically, in the Ixodidae.

Observation of the midgut of a moderately engorged tick shows the gut in constant motion, with peristaltic waves running along the caeca. This is brought about by a fine network of muscle fibers imbedded in the wall.

HINDGUT

(Fig. 2; pls. 13, 14, 23)

The hindgut, as discussed in the following section, includes that part of the alimentary canal which is posterior to the rectal tube and which consists of the following structures: the rectal sac, the Malpighian tubules, the anal canal, and the anus.

The rectal sac (r. s.) is a large membranous sac of indefinite shape situated directly over the anus. It is nearly always filled with whitish excretory material. Into its anteroventral aspect opens the rectal tube. Slightly posterior are attached the paired Malpighian tubules, and into the posteroventral aspect opens the anal canal.

In section the rectal sac is seen to be a thin-walled bladder without distinct cell outlines and only a few scattered nuclei, which are often thicker than the wall, to indicate its cellular nature. The rectal sac serves principally as a storage organ for excretory material and probably also in some degree as a water-absorbing organ.

The Malpighian tubules (t. mpg.) are paired organs opening into the floor of the rectal sac. From that point they are directed posteriorly a short distance, where they curve dorsally and extend along the viscera to the anterior lateral lobe of the midgut. At this point they are attached to the gut by several fine connective tissue fibers. From this attachment they turn toward the posterolateral margin of the body until approximately opposite their point of origin in the viscera. There they curve under the viscera and extend anteriorly to a point opposite the brain. As seen in vivisection, the Malpighian tubules vary from translucent to opaque creamy white, depending upon the quantity of excretory material present. They are in constant motion, with peristaltic waves forcing the contents back and forth. In transverse section the Malpighian tubules (pl. 13, *G*), are seen to consist of a single layer of large cuboidal cells resting upon a thin membrane. The nuclei are very large and are situated centrally. The lumen of the tube is relatively large and contains numerous small, spherical, highly refractive excretory granules. Circulation of the excretory mass within the tubule is brought about by a network of muscle fibers imbedded in the wall, similar to those found in the midgut.

The anal canal (an. can.) is a short, thin-walled tube connecting the rectum and the anus. Its walls are slightly folded, permitting an appreciable degree of distension, and are lined with a thin layer of chitin continuous with the surface of the anal valves (pl. 14, *A*).

The anus (an.) is situated on the ventral surface of the body, in the median line slightly posterior to the level of the stigmal plates. In ventral view (pl. 14, *B*) it is seen to consist of a ring of chitin, the anal anulus (an. an.), surrounding a pair of ellipsoidal valves (an. v.). The anal valves are articulated with the anal anulus through a circular elastic membrane. Between the anal valves is the anal aperture (an. ap.), a slitlike opening guarded by numerous setae inserted on the anal valves.

The anus apparently functions through the contraction of the anal muscles (m. an.), which originate on the margins of the anal valves and are inserted on the wall of the anal canal. It is likely, however, that the posteroaccessory dorsoventral body muscles (m. p. a.) assist in forcing the fecal material from the rectum.

NERVOUS SYSTEM

(Fig. 5; pl. 15)

In comparison with other closely related Arthropods, such as the insects, the nervous system of *D. andersoni* is simple. It consists of a single consolidated ganglionic mass or "brain" and a radiating peripheral system of nerve trunks. The organs of special sense will be discussed in a later section.

BRAIN

The brain (br.) is creamy white, spheroidal, slightly flattened dorsoventrally, about 0.5 mm. in width, and is situated immediately above the genital aperture. It appears to be composed of two primary masses, the dorsal and ventral ganglia, which

Fig. 5. Schematic view of the central nervous system in dorsal optical section, showing the disposition of the ganglia. (See pp. 231–232 for explanation of abbreviations used.)

are separated by the oesophagus. In transverse section it is seen that the "dorsal ganglion" (d. g. br.) actually consists of four pairs of ganglia, two pairs situated dorsally and two laterally on each side of the oesophagus. The two dorsal pairs are the cheliceral (g. ch.) and palpal ganglia (g. p.), the former being slightly anterior to the latter. On each side of these ganglia and slightly ventral in position are found the cerebral (g. c.) and pharyngeal ganglia (g. ph.), the former lying slightly dorsal to the latter. The "ventral ganglion" includes the major portion of the brain mass and consists of six pairs of ganglia. The largest of these are the four pairs of pedal ganglia (g. pd.), which are arranged lateroventrally along the margins. On the posterior margin of the "ventral ganglion" between the pedal ganglia of the fourth pair of legs are found two pairs of small visceral ganglia (g. v.).

One may readily see from the foregoing description that extreme consolidation has taken place, making it difficult to determine the original relationships of the various ganglia from their present position.

Histologically the brain is of the typical arthropodan type and consists of an inner mass of interwoven fibers, the neuropile; an outer layer of large, deeply staining ganglionic cells which surround and indicate the limits of the various ganglia; and a thin outer investing sheath, the neurilemma, which is continuous with the sheath of the nerve trunks and is also reflected around the oesophagus as it passes through the brain.

PERIPHERAL NERVES

In order to facilitate discussion the peripheral nerves may be considered in three groups, namely, the capitular nerves, the pedal nerves, and the visceral nerves.

The capitular nerves originate in the so-called "dorsal ganglion" and extend anteriorly to the capitulum. As indicated by the preceding description of the ganglia, they consist of four pairs. The cheliceral nerves (n. ch.) extend to the base of the chelicerae, where they branch; one branch enters the shaft of the chelicerae, while the other serves the retractor muscles of the chelicerae. The palpal nerves (n. p.) arise as a pair from the palpal ganglia and become fused into a single trunk shortly after leaving the brain substance. This single trunk lies directly over the oesophagus and extends about half the distance to the pharynx, where it divides, one branch entering the base of each palpus. The paired oculoporosa nerves arise from the lateral cerebral ganglia and extend anteriorly a short distance. In the female they branch, one branch continuing anteriorly to the porose area, the other appearing to innervate the eye. The pharyngeal nerves (n. ph.) arise from the lateroventral pharyngeal ganglion and extend anteriorly to the pharynx, where they branch several times and innervate the pharyngeal region of the capitulum.

The pedal nerves (n. pd.) arise from the lateral pedal ganglia and extend directly to the coxal cavities, which they enter, under the anterior margin of the coxal muscles. These are the largest nerve trunks in the body.

The two pairs of visceral nerves (n. v.) arise from the visceral ganglia between the fourth pair of pedal ganglia and extend posteriorly, giving off numerous branches, which innervate the entire viscera.
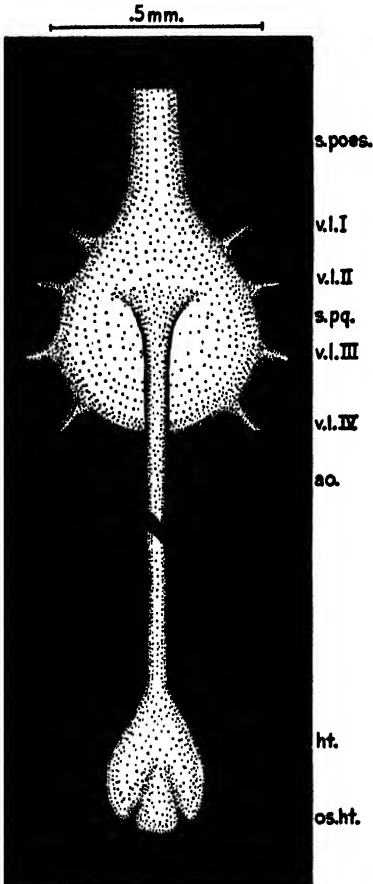
Fig. 6. Schematic dorsal view of the circulatory system. The leg veins are not shown completely. (See pp. 231–232 for explanation of abbreviations used.)

CIRCULATORY SYSTEM

(Fig. 6; pl. 24)

The circulatory system of *D. andersoni*, and other ticks as well, is somewhat more complex than is that of the insects. It consists of the following well-defined parts: the heart, dorsal aorta, periganglionic sinus, perioesophageal sinus, and blood.

HEART

The heart (ht.) is the sole pulsatile organ of the body. It is situated in the median line about two-thirds the length of the body toward the posterior margin, directly under the dorsal fovae. It is a pear-shaped organ about 0.25 mm. across the widest part and 0.38 mm. in length, bearing on the posterolateral margin two simple ostia

(os. ht.). The heart is supported and actuated by five extrinsic muscles, two pairs being inserted laterally and a single muscle attaching in the posterior portion between the ostia. These muscles originate on the ventral surface of the dorsal body wall. Diastole is accomplished by the contraction of these extrinsic muscles, and systole is brought about by the contraction of an interlaced network of intrinsic muscle fibers in the membranous wall. In action the heart simply contracts in the manner of a clinching fist: the ostia close automatically and the blood is forced into the dorsal vessel. The pulsatile rate is extremely variable; in a series of counts made at room temperature (approximately 70° F.), the rate varied from 20 to 128 per minute. Frequently, heart action ceases for several seconds.

The wall of the heart is membranous and the individual cell outlines are invisible. Its cellular nature may be ascertained only by the presence of small scattered nuclei.

DORSAL AORTA

The dorsal aorta (ao.) is merely a tubular prolongation of the heart which extends anteriorly over the dorsal wall of the stomach and communicates with the periganglionic sinus. Histologically it is identical with the heart except for the absence of muscles.

PERIGANGLIONIC SINUS

The periganglionic sinus (s. pg.) completely invests the brain and is extended around the pedal nerves into the coxal cavities. Anteriorly the periganglionic sinus is projected around the capitular nerves and oesophagus as a whole, forming the perioesophageal sinus.

PERIOESOPHAGEAL SINUS

The perioesophageal sinus (s. poes.) extends around the capitular nerves and oesophagus and continues anteriorly to the posterior end of the pharynx, where it terminates with the end open.

BLOOD

The circulating fluid, or blood, is a pale, almost colorless, slightly turbid fluid in which numerous large ameboid corpuscles are suspended (pl. 24). They contain large deep-staining nuclei in which may be seen granular aggregates. The cytoplasm has a reticulate appearance, and contains many small dark granules exactly like those found free in the blood plasma. Often the cytoplasm also contains a number of quite large spherical elements which are strongly eosinophilic and have evidently been phagocytized, since frequently they are also found free in the plasma.

MALE REPRODUCTIVE SYSTEM
(Pls. 16, 17, 25)

The male organs of reproduction consist of paired lateral testes, paired vasa deferentia, complex median accessory glands, and a single ectodermal ejaculatory duct leading to an external orifice covered by an ectodermal flap.

TESTES

The large paired testes (tes.) occupy a lateral position in the body, extending from the posterior margin of the brain to about the posterior margin of coxae IV. Near their free end they make a loop and curve toward the median line and terminate just anterior to the rectal sac. In transverse section (pl. 16, *C*) the testes appear as round tubular structures with a very small lumen, the vas eferens. Surrounding the lumen is a layer of large cyst cells, each enclosed in a thin epithelial sheath and containing a number of spermatogonia which eventually become spermatids and

finally spermatozoa. Investing the testes is a thin sheath of epithelial tissue containing small scattered nuclei. For a discussion of the process of spermatogenesis in ticks, the reader is referred to the works of Bonnet (1906a), Nordenskiöld (1920), and Warren (1931).

VASA DEFERENTIA

The vasa deferentia (v. d.) are simple paired tubes connecting the testes and ejaculatory duct. From the testes they extend posteriorly between the lobes of the accessory glands to a point near the posterior margin of the glands and are then reflected anteriorly to the posterior end of the ejaculatory duct, into which they empty. At the junction of the ejaculatory duct and vasa deferentia is the orifice of the accessory genital glands. Robinson and Davidson (1913), working with *Argas persicus*, describe and figure what they term the seminal vesicle, which receives the vasa deferentia and is surrounded by the accessory glands. No indication of such a structure has been found in the present investigation. It is possible that, owing to the immaturity of the specimens, the seminal vesicle was not developed. I am of the opinion, however, that the slight posterior expansion of the ejaculatory duct represents the seminal vesicle in *D. andersoni*.

ACCESSORY GENITAL GLANDS

The large multilobed accessory genital glands (gl. ac. gen.) rest on the floor of the body cavity posterior to the brain and receive anteriorly the vasa deferentia and the ejaculatory duct. These rather complex glands are made up of two pairs of dorsal lobes, one anterior and one posterior; two pairs of lateral lobes, one dorsal and one posterior; three pairs of ventral lobes, one pair being anterior, one lateral, and one posterior; and an unpaired median ventral lobe. The anterodorsal (l. a. d.) and posterodorsal lobes (l. p. d.) empty into the posterior portion of the ejaculatory duct. The anteroventral (l. a. v.) and posteroventral lobes (l. p. v.) fuse with the lateroventral lobe (l. l. v.), which empties directly into the unpaired medioventral lobe.

Robinson and Davidson (1913) described two types of tissue in the male accessory glands of *Argas persicus;* these were called spongy and granular. In the present investigation I have found two types of cells identical with those described by them. The two types of cells are distinct and never found mixed in the same lobe. Spongy tissue is confined to the anteroventral, lateroventral, and posteroventral lobes. The remainder of the gland is of the granular type.

Transverse sections through the spongy lobes (pl. 16, *B*) show that they consist of large, loosely aggregated cells with large, ovoid, strongly basiphilic nuclei. Toward the lumen the cells tend to become columnar with ellipsoidal nuclei. The entire lobe is invested by a thin epithelial sheath exactly like that which invests the remainder of the gland.

The granular lobes (pl. 16, *A*), on the other hand, consist entirely of columnar cells with small ellipsoidal nuclei. Toward the lumen, elaborated granular elements may be distinguished and occasionally the lumen is filled with these elements.

The accessory glands apparently have two functions, namely, to provide the thin chitinous spermatophore in which the spermatozoa are conveyed to the female, and to supply nourishment to the spermatozoa during their stay within the spermatophore.

EJACULATORY DUCT

The ejaculatory duct (ej. d.) consists of a simple flattened tube extending anteroventrally from the accessory glands to a point under the brain where it opens on

the body surface. Being of ectodermal origin, it is lined with a thin chitinous intima which is continuous with the external surface of the body. The anterior end of the duct is protected by a posteriorly projecting flap of ectoderm (pl. 16, *D*).

In transverse section the ejaculatory duct is semiellipsoidal, tending to become broader at the posterior end. The chitinous intima rests upon a single layer of small cells like the epidermal cells. These in turn rest upon a thin basement membrane.

FEMALE REPRODUCTIVE SYSTEM
(Pls. 18, 19, 26)

The female organs of reproduction include a single ovary with paired oviducts, a common oviduct, seminal receptacle, vagina, accessory glands, and an ovipositing structure—Gené's organ.

OVARY

The single ovary (ov.) extends posteriorly from one oviduct to the posterior margin of the rectal sac, where it curves anteriorly and across the anterior margin of the rectal sac and thence posteriorly again to the posterior margin of the rectal sac, finally recurving anteriorly and connecting with the other oviduct. In the sexually immature specimens used in this investigation the ovary appeared as a smooth, creamy white structure and did not show the irregularities caused by developing ova which have been figured by other authors.

When free from the pressure of surrounding tissues, the ovary assumes a nearly round shape in transverse section. It consists of two cellular layers, the outer made up of ova (o.) in various stages of development, and the inner layer consisting of epithelial tissue (ep. ov.). The ova may be of almost any size: the small ones tend to be cuboidal; the larger, more ovoid or columnar. The nuclei of the ova are spherical, and contain aggregates of granules which are slightly basiphilic. The protoplasm is quite homogeneous, with a few small scattered granules. The ova rest on a thin layer of epithelial cells the outlines of which are made out with difficulty. The nuclei are frequently thicker than the cellular layer itself.

OVIDUCTS

The oviducts (d. ov.) extend from the ovary anteriorly to a point opposite the posterior margins of the vagina, where they are reflected posteriorly almost to the ovary and then curve anteriorly under the seminal receptacle and empty into an expanded sacculate common oviduct ventral to the cervical portion of the vagina. In transverse section the oviducts are seen to consist of three layers, namely, a thin outer sheath of epithelial cells similar to the epidermal cells, a central layer of muscle fibers, and an inner sheath of elongate epithelial cells which protrude into the lumen. These last-named cells have a large polyhedral nucleus nearly filling the cell.

COMMON OVIDUCT

The paired oviducts pass anteroventrally around the seminal receptacle and empty into a small expanded structure which has arbitrarily been called the common oviduct (d. com. ov.). A similar structure in *Boophilus annulatus* was termed the "receptaculum seminis" by Williams (1905). However, the observation of spermatophores in the "uterus" of *Argas persicus* by Robinson and Davidson (1913), an organ which is the same in structure and position as the receptaculum of *D. andersoni*, would indicate that Williams's term is a misnomer. The common oviduct cannot expand as far as the receptaculum, and it is not situated in a position where

it can expand without seriously displacing the other organs of the reproductive system. Anteriorly, the common oviduct forms a short rounded tube which empties into the anteroventral portion of the cervical vagina.

SEMINAL RECEPTACLE

The seminal receptacle (rec. sem.) is an unpaired sac situated in the median line between the stomach and ventral body wall. Its anterior portion appears to be produced around the posterior portion of the cervical vagina. The wall of the receptaculum is made up of columnar epithelial cells which are greatly folded and compressed when it is empty, rendering it extremely difficult to make out the cell outlines. The nuclei are small, mildly basiphilic, and arranged in a haphazard manner. Few muscle fibers are to be seen in its walls. From its size and structure it apparently functions as a place of storage for the spermatophores. That it is capable of great distension is shown by the observations of Robinson and Davidson (1913), who have noted as many as eight spermatophores in the "uterus" at the same time. Occasionally, in the course of a dissection, the receptaculum will become filled with dissecting fluid and take on the appearance of a large thin-walled bladder.

VAGINA

The vagina includes that portion of the female reproductive system which extends from the external orifice to the seminal receptacle; it receives the common oviduct and ducts of the accessory genital glands and is divided into two distinct parts: an anterior or vestibular portion (vg.), and a posterior cervical portion (vg.') which appears to be inserted into the seminal receptacle.

The posterior portion of the vagina is a short barrel-shaped organ similar in structure to the seminal receptacle except that it does not show so much irregular folding. The nuclei are regularly arranged at the base of the cells. Surrounding this portion of the vagina is a heavy layer of circular muscle fibers (m. vg.) which presumably aid in extruding the egg. Also attached to this organ, on its antero-dorsal aspect, is a heavy band of muscle fibers which are directed anteroventrally and attach to the ventral body wall slightly anterior to the genital orifice. It may be seen how these muscles, with the aid of the dorsoventral body muscles, could force an egg from the vestibular portion of the vagina to the exterior.

The vestibular portion of the vagina is a simple, dorsoventrally flattened, tubular organ similar in structure to the cervical portion but without so thickly folded an epithelial layer. It is, however, somewhat folded so as to allow considerable distension. The posterior portion of the vestibular vagina projects slightly into the cervical portion, and their walls gradually blend together. It is at this point that the common oviduct enters, on the ventral aspect.

ACCESSORY GENITAL GLANDS

In contrast with those of the male, the accessory genital glands (gl. ac. gen.) of the female are extremely simple, consisting of a pair of short sausage-shaped tubes which empty into the dorsoanterior aspect of the cervical portion of the vagina. They consist of a single layer of columnar cells with large conical nuclei and a very small lumen. It is presumed that the function of the accessory glands is to provide lubrication for the passage of the egg through the vagina. I have not myself observed the process of oviposition. Robinson and Davidson (1913) state that in Ixodid ticks the vestibular portion of the vagina is completely extruded, forming a short truncate ovipositor.

GENÉ'S ORGAN
(Pl. 19)

Gené's organ (Gen. org.) was discovered by Gené (1844) and named after its discoverer by Nuttall (1908). It is a bilobed structure lying under the scutum and communicating with the exterior through a transverse slit in the camerostomal fold. Attached to the posterolateral aspect of each lobe is a gland (gl. Gen. org.) which apparently supplies a mucilaginous substance. In transverse section the eversible portion of the structure is seen to consist of an inner chitinous sac (ct. s.) continuous with the integument, and an outer hypodermal sheath (hd. s.) similar to the hypodermis of the integument. Attached to the posterior end of each lobe is a bundle of longitudinal muscle fibers which originate on the posteroventral margin of the scutum. These presumably act as retractors. The exact method by which the chitinous sac is everted is not known. It is supposed, however, that this may be accomplished through the pressure of the blood brought about by the contraction of the dorsoventral body muscles. When extruded, Gené's organ appears as a bidigitate glistening sac which grasps the eggs from the protruded vagina and carries them back onto the dorsum. For a discussion of oviposition in ticks, I would refer the reader to the works of Nuttall (1908), Samson (1909), Wheler (1906), and Lewis (1892).

Copulation was not observed during the course of this investigation. However, it is assumed to be essentially the same for all species. The works of Nuttall and Merriman (1911) and Lewis (1900) give detailed consideration to this function.

RESPIRATORY SYSTEM
(Pl. 20)

The respiratory system consists of paired external spiracles and an internal system of ramifying tracheal tubes. This system is essentially the same for all ticks and has been described completely or partly by Bonnet (1907), Nuttall, Cooper, and Robinson (1908), Nordenskiöld (1909), and Samson (1909).

SPIRACLES

The spiracles (sp.) are on the ventral body surface near the lateral margins and slightly posterior to the fourth coxa. In surface view (pl. 20, *A*) they appear as oval plaques with a posterolateral prolongation which is somewhat longer in the male than in the female. The major portion of the spiracular surface is made up of globular cells, forming the area porosa (a. por.), each with an external pore. In the central portion of the area porosa is a chitinous oval plate, the macula (mac.), in which is situated a crescentic slitlike opening, the ostia (os.). In transverse section (pl. 20, *C*) it is seen that the ostia opens into a chamber, the atrium (at.), from which arise the primary tracheal trunks. Surrounding the atrium and communicating with it is a chamber, the periatrial space (p. sp.), which in turn communicates with the goblet cells, thus establishing a passage for air via the area porosa. The area porosa consists of three layers: an external layer of goblet cells (gob.), a middle layer of chambers (ct. c.) formed by the pedicels supporting the goblets, and an inner chitinous layer, forming the stems of the goblets (st. gob.) through which pass fine pores containing protoplasmic strands produced from the hypodermal cell layer. For a more detailed account of the microscopic character of these structures, see the excellent work of Stiles (1910).

Attached to the dorsolateral surface of the atrium is a muscle which extends toward the median line and originates on the inner surface of the dorsum. This is thought to function as an aid in closing the tracheal system.

TRACHEAL TRUNKS

Arising from the atrium are five tracheal trunks (pl. 20, *B*), which are disposed as follows. (1) A large anterior trunk (tr. ant.) extends anteriorly along the lateral margins of the body, giving off branches which enter each leg, and providing tracheae for the brain, mouthparts, and the anterior portion of the body generally. (2) Arising posteriorly to the anterior trunk is the anterior median trunk (tr. ant. med.), which provides tracheation for portions of the salivary glands, reproductive system, and so forth. (3) Posterior to the anterior median trunk is the posterior dorsal trunk (tr. post. dors.), which provides tracheation for portions of the midgut, salivary glands, and reproductive system. (4) The next trunk posteriorly is the posterior median (tr. post. med.), which, with the posterior lateral trunk (tr. post. lat.), supplies the posterior portion of the viscera in general.

The only difference in the tracheal system of the sexes lies in the number of tracheal tubes, the female having many more than the male.

Histologically the tracheae are identical with those found in insects. They consist of an outer hypodermal layer and an inner chitinous layer in which is imbedded a chitinous spiral thickening, serving presumably to maintain their patency.

For a discussion of respiration in ticks and function of the spiracles, see the work of Mellanby (1935). On the basis of experimental evidence, Mellanby concludes: (1) that a closing mechanism is present, (2) that the physiological reaction governing the process is similar to that in insects, (3) that at room temperature the spiracles are closed most of the time, the animal probably breathing through the area porosa, and (4) that water is lost from the tracheae, the cuticle being relatively impervious.

MUSCULAR SYSTEM
(Fig. 7)

To facilitate discussion, the muscular system may be divided into four parts: first, the muscles of the capitulum, including the mouthparts, which were described under "External Anatomy"; second, the muscles of the viscera, which were discussed in connection with the organs to which they were attached; third, the muscles of the legs; and fourth, the muscles of the body.

LEG MUSCLES

The muscles of the legs consist of a pair in each segment, a tensor and a flexor. The coxae are rigidly applied to the body wall and contain a large flexor and tensor which are inserted on the trochanter, causing it to rotate in an arc in the manner of a human shoulder joint. The muscles of the other segments are arranged to produce articulation only in one plane, as in the human elbow joint. The muscles of the tarsus are attached to tendons which are inserted on the basal articulation of the pulvillus and allow movement in a single plane.

BODY MUSCLES

The muscles included here are all dorsoventral; that is, they originate on one surface of the body and are inserted on the other surface. They fall naturally into three groups: the marginal muscles (m. mg.), the genital muscles (m. gen., m. gen.'), and the posterior muscles (m. p. a., m. p. m.).

The marginal dorsoventral body muscles are inserted in four groups on the lateral margins of the coxal cavities. From that point they extend somewhat obliquely to their origin on the dorsal body wall. The most anterior of these muscles originate near the lateral margin of the anterior portion of the cervical groove, and the others

Fig. 7. *A*, Schematic dorsal view of the floor of the body cavity, showing the attachment of the principal body muscles. *B*, Diagram of the male scutum, showing the principal unsilvered areas and the muscles which attach to them. (See pp. 231–232 for explanation of abbreviations used.)

originate in a series of three pairs of unsilvered spots on the dorsum of the male and in a corresponding position in the female. These muscles apparently function as accessories, in promoting the flow of body fluid, during defecation, and perhaps also as an aid to tracheal ventilation.

The genital muscles are all inserted on the genital groove and may be divided into two groups: the anterior genital muscles (m. gen.), which are inserted laterally with respect to the genital orifice; and the posterior genital muscles (m. gen.'), which are inserted posterior to the genital orifice and laterally with respect to the accessory glands in the male or the seminal receptacle and cervical vagina in the female. The anterior genital muscles pass obliquely through the viscera in a dorso-posterolateral direction and originate slightly posterior to the arms of the cervical grooves. The posterior genital muscles likewise pass through the viscera in an oblique dorsoposterolateral manner and originate laterally with respect to the dorsal fovae. The primary function of the genital muscles appears to be, in the female, the extrusion of eggs, and in the male, the extrusion of spermatophores. They may also serve in a manner similar to that of the marginal muscles.

The posterior dorsoventral body muscles include a pair of bundles inserted laterally with respect to the anus, the posteroaccessory dorsoventral body muscles (m. p. a.); and a single group inserted posterior to the anus, the posteromedian dorsoventral body muscles (m. p. m.). The former extend in a dorsolateral direction and originate posteromesially with respect to the posterior pair of marginal muscles. The posteromedian dorsoventral body muscles pass in a direction dorsoposterior to their origin between the origins of the posteroaccessory muscles. It seems quite obvious from the position of these muscles around the rectal sac that they serve primarily to force the excrement into the anal canal and out of the body, and perhaps secondarily to promote ventilation and the flow of body fluid.

For a discussion of the musculature of the Ixodidae in general see the work of Ruser (1938), which includes an extensive bibliography.

ORGANS OF SPECIAL SENSE
(Pl. 21)
EYES

The two eyes (pl. 21, *G*) are on the lateral margin near the angle formed by the margin of the body and the margin of the scutum. Superficially they appear as small, colorless, convex lenses. In section they are shown to be simple structures. The lens is merely a hyaline portion of the integument and has a typical hypodermal cell layer. Under the hypodermal layer, at one side of the lens, is a group of large nerve cells (pl. 21, *H*) the fibers of which may be traced to the brain. No structure or pigmentation was discovered in the lens. Bonnet (1906), however, described perpendicular striae accentuated by black pigment and stated that the hypodermis was prolonged to form a vitreous body surrounded by an area of compressed cells forming an irisated zone.

There is probably little doubt that the so-called eye is a photoreceptive organ, but it requires considerable imagination to assign to it any image-forming properties. A number of investigators have advanced the belief that the photoreceptive property is generally distributed over the body, and in the eyeless Argasids this is apparently true, since it has been shown that they are responsive to photostimulation.

PITS AND HAIRS

Sensory pits and hairs are quite generally distributed over the dorsal surface in both sexes. The mouthparts, legs, genital orifice, and anal orifice possess many of

these structures also. They are similar in structure to the sensory pits and spines so commonly found on insects. In transverse section a sensory hair (pl. 21, *F*) consists of a curved hollow shaft set on a thin membrane in a depression of the epidermis. In the communicating epidermal pore is a nerve cell which is connected with the hollow shaft of the hair by protoplasmic strands and with the nervous system by fine nerve fibers. These hairs are presumably tactile in function.

Although they are constructed on the same principle as the sensory hairs, the sensory pits differ in some respects. In transverse section (pl. 21, *I*) they appear as truncate cones suspended by a thin circular membrane in a rather deep depression in the epidermis. The conelike portion is solid, but at its lower end it is attached to a sensory cell as in the sensory hairs. The function of the sensory pits is not known.

POROSE AREAS

These peculiar structures are found only in the female, as paired, oval, cribiform areas on the dorsal surface of the basis capituli. In section (pl. 21, *E*) it appears that the epidermis is somewhat thinner and is pierced by many fine pores, each containing a sensory cell with protoplasmic processes and nerve fibers similar to those found in the sensory pits and hairs. The hypodermal layer is without modification.

The function of the porose areas is not known. It would seem likely, however, that they serve in some secondary sexual capacity since they are found only in the female.

DORSAL FOVAE

These organs are found, in both sexes, on the dorsal surface about two-thirds the length of the body toward the posterior margin. Superficially (pl. 21, *A*) they appear as pale yellow, punctate, circular areas about 0.07 mm. in diameter and 0.2 mm. apart. Each fova is pierced by approximately twenty-five fine pores. In section (pl. 21, *B*) the fovae are seen to be about one-half the thickness of the surrounding epidermis. Each pore contains a protoplasmic process extending from a nerve cell below. The nerve cells also give off fibers which coalesce and may be traced to the brain.

The function of these organs is likewise unknown. It is perhaps significant that they are situated directly over the heart; possibly they serve as a regulator.

HALLER'S ORGAN

This organ was first described by Haller (1881), who thought it was auditory in function. Nuttall, Cooper, and Robinson (1908*a*) subsequently redescribed it, and somewhat later Hindle and Merriman (1912) definitely established its function as olfactory.

Haller's organ is situated on the dorsal surface of the tarsal segment of the first pair of legs. It consists of a small chamber containing numerous sensory spines and communicating with the exterior by means of a slitlike pore (pl. 21, *C, D*). Its detailed character has been described by Nuttall, Cooper, and Robinson (1908*a*) in the Ixodoidea as a whole, and hence it will not be necessary to consider that aspect here.

By removing this organ Hindle and Merriman were able to induce *Argas persicus, Ornithodoros moubata,* and *Hyalomma aegyptium* to feed on a variety of non-biological substrates including solutions of gelatin, sodium chloride, and sodium citrate. Totze (1933, 1934) has confirmed and extended these observations.

ACKNOWLEDGMENT

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EXPLANATION OF ABBREVIATIONS USED

a. ph. v.—alae of the pharyngeal valve
a. por.—area porosa of the spiracle
an.—anus
an. an.—anal annulus
an. ap.—anal aperture
an. can.—anal canal
an. v.—anal valve
ao.—aorta
art.—articulation of internal article
at.—atrium
b. c.—basis capituli
br.—central nerve mass, or brain
buc. cav.—buccal cavity
cam. f.—camerostomal fold
cer. gr.—cervical groove
ch.—chelicera
ct. c.—chitinous cells supporting goblet layer of spiracle
ct. s.—chitinous sac of Gené's organ
cx.—coxa
d. ch.—digit of chelicera
d. com. ov.—expanded common oviduct
d. fov.—dorsal fova
d. g. br.—dorsal ganglion of brain
d. ov.—oviduct
d. p.—dorsal process
d. sal.—salivary duct
e. a.—external article
ej. d.—ejaculatory duct
ep. ov.—ovarian epithelium
fes.—festoons
fm.—femur
g. c.—cerebral ganglion
g. ch.—cheliceral ganglion
g. p.—palpal ganglion
g. pd.—pedal ganglion
g. ph.—pharyngeal ganglion
g. s. a.—granule-secreting alveoli
g. v.—visceral ganglion
gen. ap.—genital aperture
gen. gr.—genital groove
Gen. org.—Gené's organ
gl. ac. gen.—accessory genital glands
gl. Gen. org.—glandular portion of Gené's organ
gl. sal.—salivary glands
gob.—goblet cells of spiracle
h.—hypostome
h. g.—hypostomal gutter
Hal. org.—Haller's organ
hd. s.—hypodermal sac of Gené's organ
ht.—heart
i. a.—internal article
l.—leg
l. a. d.—anterodorsal lobe of accessory genital glands
l. a. v.—anteroventral lobe of accessory genital glands
l. d. l.—dorsolateral lobe of accessory genital glands

l. l. v.—lateroventral lobe of accessory genital glands
l. m. v.—medioventral lobe of accessory genital glands
l. ov.—lumen of ovary
l. p. d.—posterodorsal lobe of accessory genital glands
l. p. l.—posterolateral lobe of accessory genital glands
l. p. v.—posteroventral lobe of accessory genital glands
m. an.—anal muscles
m. c. ph.—constrictor muscles of pharynx
m. c. ph. v.—constrictor muscles of pharyngeal valve
m. c. prov.—constrictor muscles of proventricular fold
m. cx.—coxal muscles
m. d. c.—depressor muscles of capitulum
m. d. ph.—dilator muscles of pharynx
m. e. d.—extensor muscles of digit
m. f. d.—flexor muscles of digit
m. gen.—anterior genital muscles
m. gen'.—posterior genital muscles
m. l. c.—levator muscles of capitulum
m. mg.—marginal dorsoventral body muscles
m. p. a.—posteroaccessory dorsoventral body muscles
m. p. m.—posteromedian dorsoventral body muscles
m. r. ch.—retractor muscles of chelicerae
m. vg.—muscular layer of vaginal wall
mac.—macula of spiracle
mar. gr.—marginal groove
n. ch.—cheliceral nerve
n. o-p.—oculoporosa nerve
n. p.—palpal nerve
n. pd.—pedal nerve
n. ph.—pharyngeal nerve
n. v.—visceral nerve
o. t. mpg.—orifice Malpighian tubule
oes.—oesophagus
os.—ostium of spiracle
os. ht.—ostium of heart
o.—ovum
ov.—ovary
p.—palp
p. sp.—periatrial space
ph.—pharynx
por. ar.—porose area
pr. f.—proventricular fold
pts.—protarsus
r. s.—rectal sac
r. t.—rectal tube
rec. sem.—seminal receptacle
s. ch.—outer sheath of chelicerae
s. ch'.—inner sheath of chelicerae
s. pg.—periganglionic sinus
s. poes.—perioesophageal sinus
scap.—scapula

scut.—scutum
sp.—spiracle
st.—stomach
st. gob.—stems of goblet layer of spiracle
sty.—oral stylet
sub. ch. p.—subcheliceral plate
t. e. d.—extensor tendon of digit
t. f. d.—flexor tendon of digit
t. mpg.—Malpighian tubule
tb.—tibia
tch.—trochanter
tes.—testis

tr. ant.—anterior tracheal trunk
tr. ant. med.—anterior median tracheal trunk
tr. post. dors.—posterior dorsal tracheal trunk
tr. post. lat.—posterior lateral tracheal trunk
tr. post. med.—posterior median tracheal trunk
ts.—tarsus
v. d.—vas deferens
v. l.—leg vein
v. ph.—pharyngeal valve
vg.—vagina, vestibular portion
vg.'—vagina, cervical portion

PLATES

PLATE 8

A. *D. andersoni,* female, dorsal view.
B. *D. andersoni,* female, ventral view.

A

B

.

B

PLATE 10

Transverse sections through the mouthparts.

A. At the level of the cheliceral digits.
B. Slightly posterior to *A.*
C. At the level of the fusion of the hypostome and basis capituli.
D. Through the basis capituli slightly anterior to the pharyngeal valve.

s.ch

d ch

h.

p III

p IV

s.ch'

c

A

B

ch

a.b.c

sub.ch p.

buc cav.

sty.

h g.

C

D
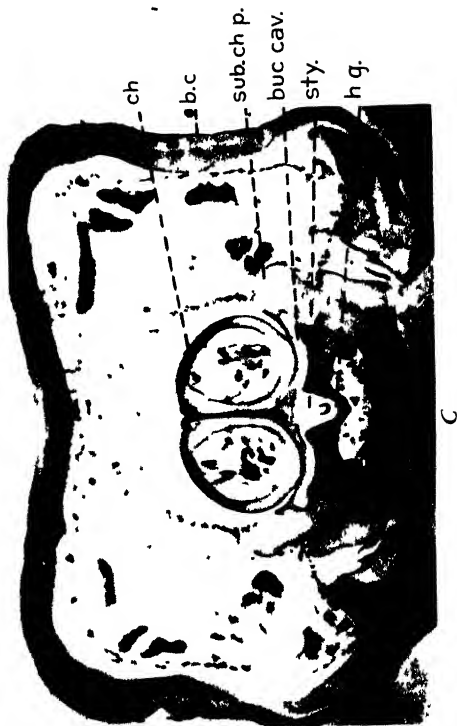
PLATE 11

A. Lateral view of the tip of a chelicera showing the digits.
B. Lateral view of an entire chelicera.

A

B
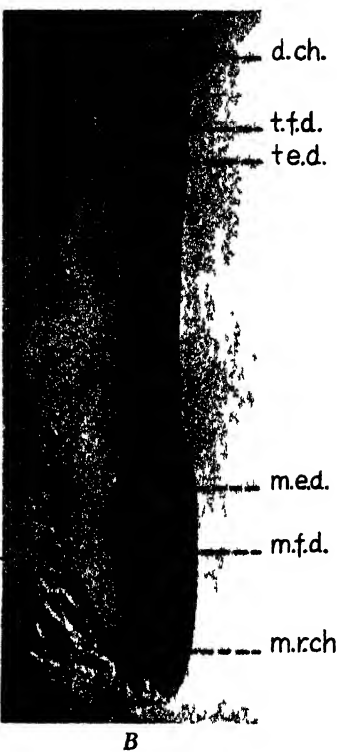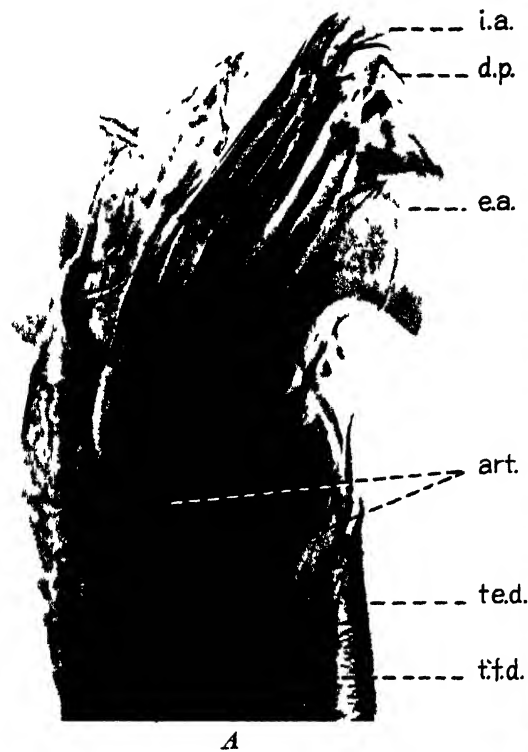
PLATE 12

A—F. Series of transverse sections through the oral stylet.
G—H. Transverse sections through the pharyngeal valve.
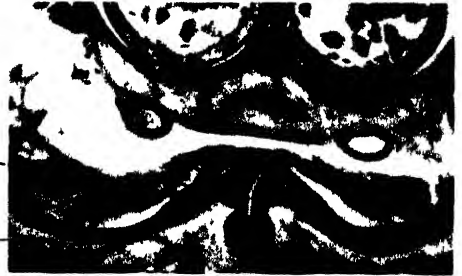
PLATE 13

A. Transverse section through the pharynx.

B. Transverse section through the proventricular fold.

C. Transverse section through the perioesophageal sinus showing the capitular nerve trunks and oesophagus.

D. Transverse section through an intestinal diverticulum.

E. Transverse section through the rectal tube slightly posterior to the stomach.

F. Transverse section through the rectal tube at its junction with the rectal sac. Note the obliteration of the lumen.

G. Transverse section through a Malpighian tubule.

A

ch
d sal
m c ph
ph
a ph v
m d ph
m c ph

B

st

mc prov

br

C

n ch
n p
n ph
oes

D

E

F

G

A

mpm

an can
m an
an an
an v
an ap

B

an an
an v
an ap

C

D

E

A

E

B

F

C

G

D

H

PLATE 16

A.   Transverse section through a granular lobe of the male accessory genital glands.

B.   Transverse section through a spongy lobe of the male accessory genital glands.

C.   Transverse section through a testis showing the arrangement of the cysts and spermatogonia.

D.   Longitudinal section through the ejaculatory duct showing the genital orifice with its ectodermal flap.

A

B

C

D

vq.

rec.sem.

vq.'

A

ql.ac.qen.

rec.sem.

m.vq.

vq.'

d.ov.

B

o.

ep ov.

l.ov.

PLATE 19

A. Transverse section showing one-half of Gené's organ.
B. Transverse section through the midportion of Gené's organ.
C. Longitudinal section through Gené's organ.

cts.

hd.s.

ql.Gen.org.

A

Gen.org.

ch.

ph

B

Gen.org.

C
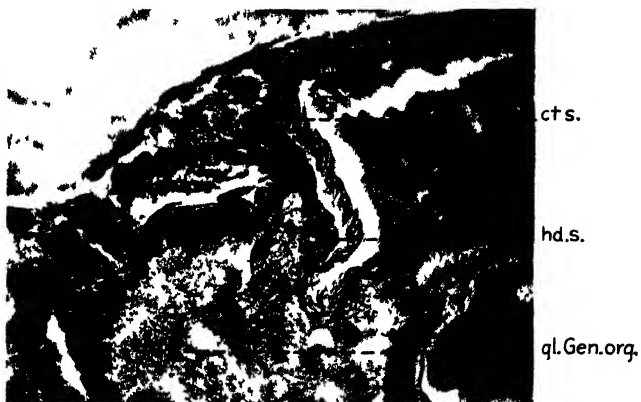
A. Optical section of a spiracular plate. The vertical division represents the plane of section shown in *C*.

B. Diagrammatic dorsolateral view of a spiracular plate showing the principal tracheal trunks.

C. Transverse section through a spiracular plate.

D. Ventral view of the tip of the hypostome, showing the recurved teeth.

E. Section through the integument of an unengorged female.

A

os.

mac.

a por.

D

tr. ant.   tr post dors.   tr. post. lat.
        tr. ant med.   tr. post med.

at.

B

E

at.

p.sp

st qob.

ct c.

qob.

mac.

os.
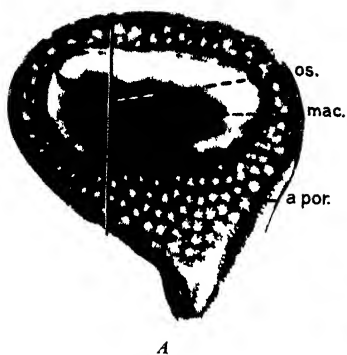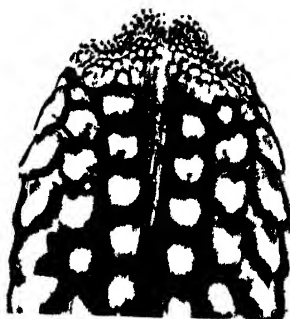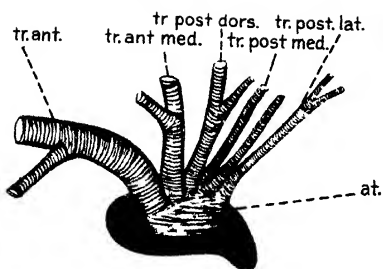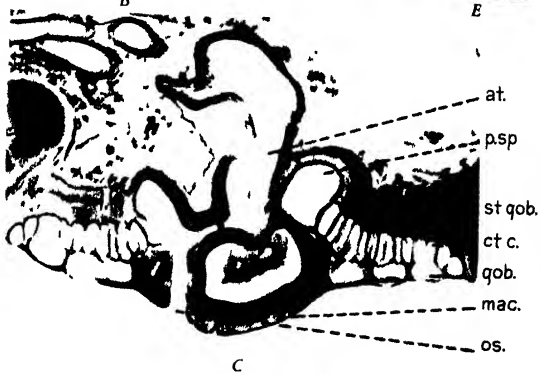
C

PLATE 21

A.   Dorsal view of the dorsal fovae of a female.
B.   Longitudinal section through a dorsal fova.
C.   Optical longitudinal section of Haller's organ.
D.   Transverse section through the pit of Haller's organ.
E.   Longitudinal section through a porose area.
F.   Longitudinal section through a sensory hair.
G.   Transverse section through an eye.
H.   Enlarged view of the sensory cells shown in the rectangle of *G*.
I.   Longitudinal section through a sensory pit.

Semischematic external views of the capitulum.

A.   Dorsal view with the palpi removed.
B.   Ventral view with the palpi removed.
C.   Dorsal view complete.
D.   Lateral view with the palpi removed.

.

h.

d.ch.

s.ch.

b.c.

A

B

p. III

p. II

p. I

C

D

.5mm.
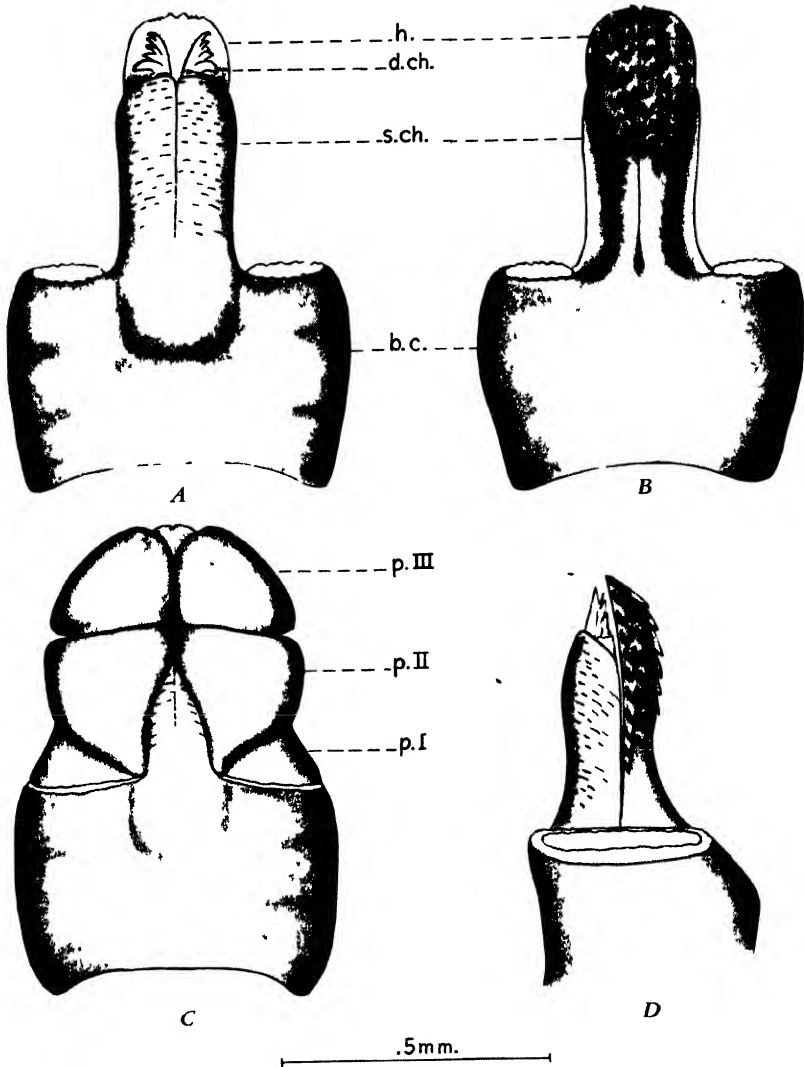
PLATE 23

Semischematic dorsal view of the digestive system. To avoid confusion the alae of the pharyngeal valve, the right salivary gland and Malpighian tubule, and left side of the midgut, have been omitted.
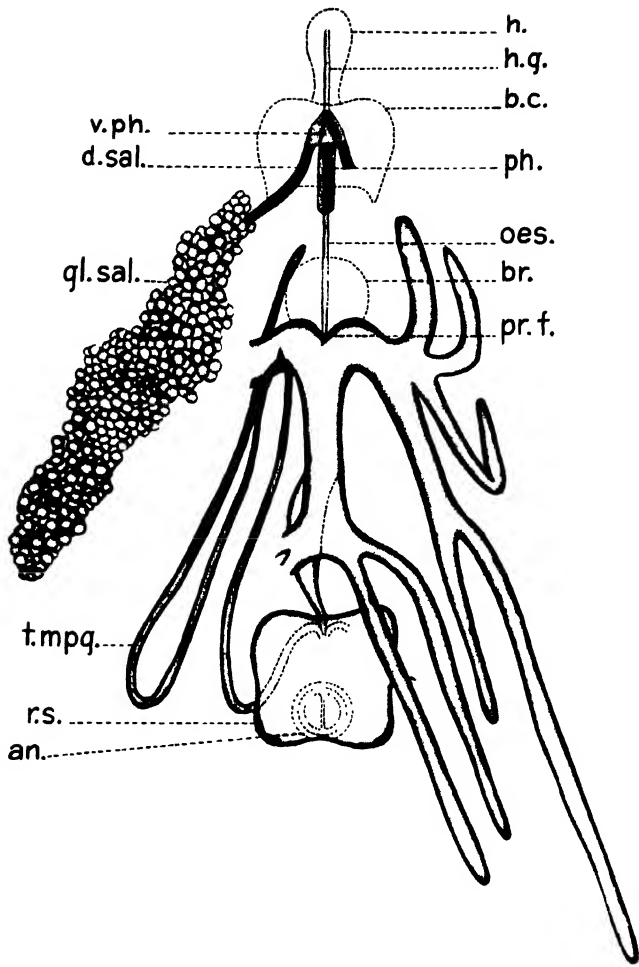
A

B

C

D

20μ
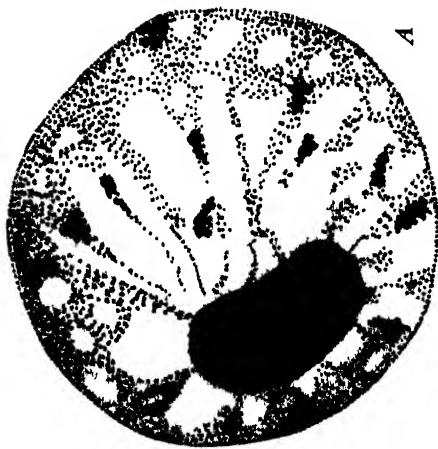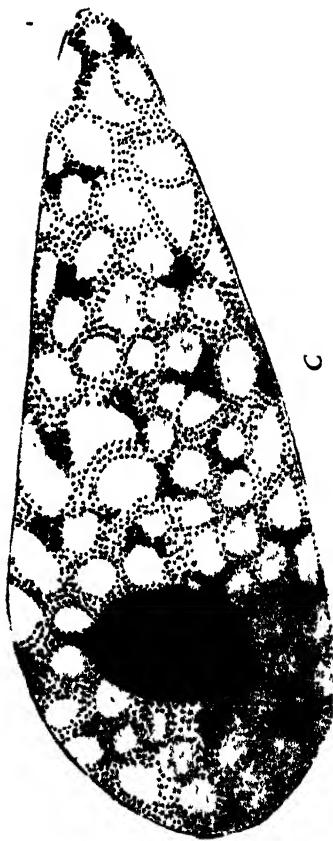
PLATE 25

Semischematic external views of the male reproductive system.

    A.   Lateral view of the accessory genital glands.

    B.   Dorsal aspect of the entire system.

A

B
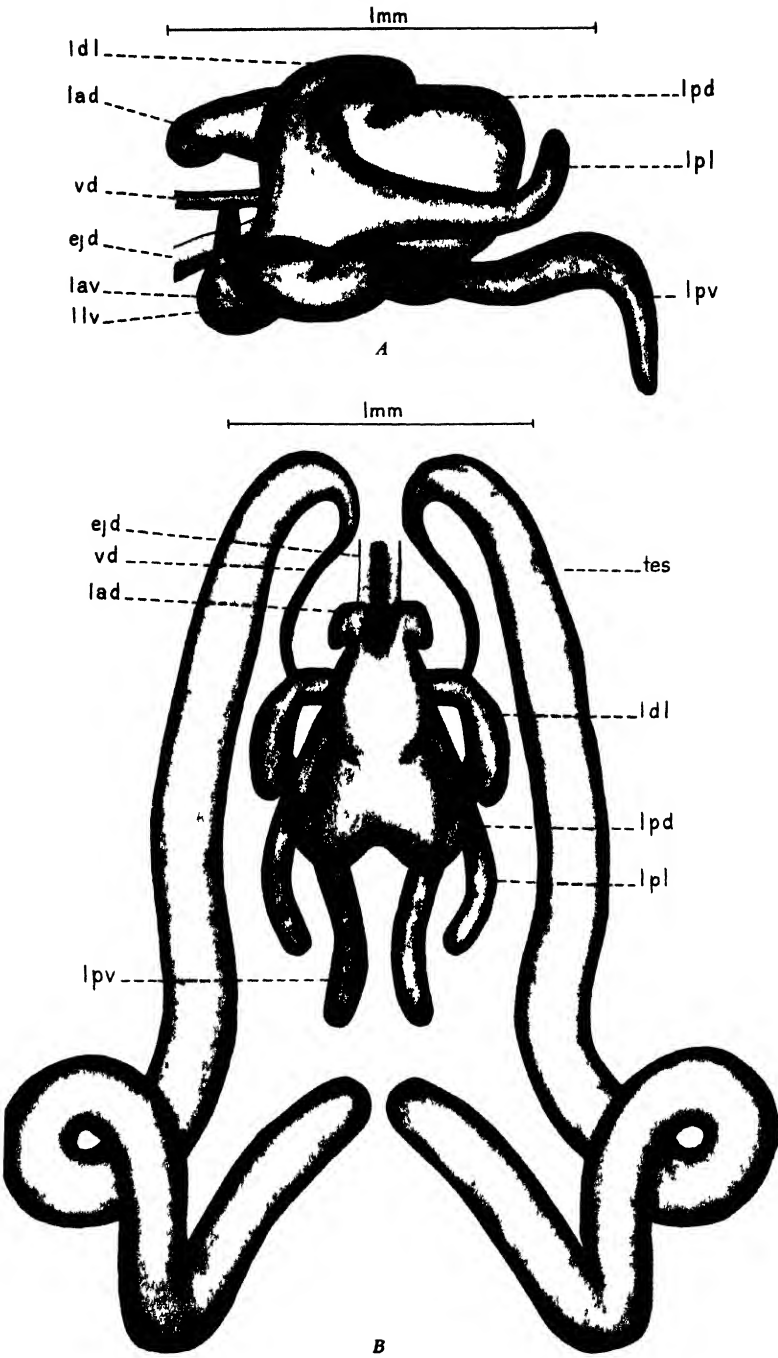
PLATE 26

Semischematic external views of the female reproductive system.

A. Lateral aspect with the ovary omitted.

B. Dorsal aspect of the entire system.

A

B

STUDIES ON THE ANOPHELINE COMPLEX OF WESTERN AMERICA

BY

THOMAS H. G. AITKEN

<div style="text-align: center;">CONTENTS</div>

STUDIES ON THE ANOPHELINE COMPLEX
OF WESTERN AMERICA

BY

THOMAS H. G. AITKEN

INTRODUCTION

FEW STUDIES in recent years have so aroused the interest of workers in the fields of culicidology and malaria epidemiology as have the investigations of the problem of European malaria. Numerous areas of high anopheline density existed, but the malaria picture did not always conform to it. In an attempt to account for the spotty distribution of the disease when the common vector, *Anopheles maculipennis* Meigen, was everywhere abundant, investigators discovered that the species was a complex consisting of a number of subspecies, only a few of which were found to be dangerous transmitters of the disease. Thus the term "anophelism without malaria" came into general usage. By means of a detailed study of the habits of the various members of a species complex, there was found a promising new approach to the problem of malaria control. I refer the reader to the works of Hackett (1937) and Swellengrebel and de Buck (1938) for complete treatises on the subject.

Anopheles maculipennis has now been broken down into six or more subspecies. Two of these, *Anopheles maculipennis atroparvus* van Thiel and *A. maculipennis labranchiae* (Falleroni), are generally considered "anthropophilic" in feeding habits (as shown by the precipitin test) and hence dangerous malaria transmitters. However, *A. maculipennis atroparvus* appears to be intermediate in position, being "zoöphilic" over a wide part of its range, yet it sometimes invades houses and regularly obtains human blood (Hackett and Missiroli, 1935). On the other hand, the remaining subspecies are primarily "zoöphilic" and do not usually transmit malaria.

Intensive study by many workers has failed to show any satisfactory method of separating the subspecies except by the structure and the markings of the eggs; Falleroni (1924, 1926) was the first to recognize that differences existed in the eggs and established the two forms now known as *A. maculipennis labranchiae* and *A. maculipennis messeae*. At present the complex can be divided on the basis of egg pattern into the dangerous and the usually harmless forms; the former, consisting of *A. maculipennis atroparvus* and *A. maculipennis labranchiae* have uniformly patterned eggs, while the latter, *A. maculipennis maculipennis*, *A. maculipennis messeae*, and *A. maculipennis melanoon* and its variety *subalpinus* Hackett and Lewis, are the barred-egg types. Additional but usually variable characters are to be found in the larval chaetotaxy and the male terminalia; also, differences are now recognized in the biologies of the various subspecies.

Roubaud (1920, 1921, 1928), was one of the first scientists to suggest a biological differentiation, which concerned different host preferences between groups of insects belonging to the same species, when he proposed his "maxillary index" theory to explain the peculiar subsidence of malaria in Europe. The theory is based on the competition for food among the anophelines: the buccal armature of paucidentate forms, having a maxillary index below 14 teeth, is too weak to pierce thick-skinned animals, and the forms are forced to feed on man and other thin-skinned animals. Those having a dental armature with an average between 14 and 15 feed on thick-skinned animals and hence are zoöphilous. When the index rises above 15, the excess competition forces a part of the population back upon man and they become dan-

gerous once more. This theory has not been found to be entirely satisfactory and the more plausible explanations of Hackett and Swellengrebel are now being investigated.

Subsequent to this initial European work, investigators throughout the world have undertaken similar studies of widespread anopheline complexes which also have varying malaria-transmitting powers. Work in India (Sweet and Rao, 1937, 1938 and Rao, Sweet, and Subba Rao, 1938) indicates that *Anopheles stephensi* Liston is composed of two forms, which have been designated *Anopheles stephensi stephensi* and *A. stephensi mysorensis* with evidence pointing to the former being a good malaria carrier. Del Vecchio (1939a,b) considers that on the basis of differences in the intercostal membrane of the egg floats there are two additional forms of *Anopheles claviger* Meigen (*bifurcatus* Meigen) in Italy: *A. claviger missiroli* Del Vecchio and *A. claviger petragnani* Del Vecchio.

In the New World several species have been similarly studied. Much of this work has been going on in South America, where the perplexing subgenus *Nyssorhynchus* is rapidly undergoing expansion, as for example, in the following: *Anopheles darlingi paulistensis* Galvão, Lane, and Corrêa (1937) ; *A. albitarsis brasiliensis* (Chagas) 1907, Root (1926); *Anopheles albitarsis limai* Galvão and Lane (1937) ; *A. oswaldoi metcalfi* Galvão and Lane (1937) (see also Townsend, 1933; Rozeboom, 1937; Galvão and Barretto, 1938).

In this country an article by King (1939) indicates that *Anopheles crucians* Wiedemann is composed of three forms, *Anopheles crucians crucians, A. crucians georgianus* King, and *A. crucians bradleyi* King; *bradleyi* breeds in brackish water, the other two in fresh water (see also Bellamy, 1939). *Anopheles walkeri* Theobald appears to be composed of two races, "northern" and "southern." Bradley (1936a,b) found constant differences in the larvae as well as fairly reliable adult characters. Hinman (1936), in an attempt to discover races of *Anopheles quadrimaculatus* Say, was unable to find any egg differences in hibernating forms in Louisiana.

In California three anophelines have been recognized by Freeborn (1926) : *Anopheles maculipennis, A. pseudopunctipennis* Theobald, and *A. punctipennis* (Say). Because of the widespread interest in the races or subspecies of anophelines and because of the necessity for accurate knowledge of these disease-bearing insects, I undertook the investigation of the possibility of such complexes existing in the California fauna; all three species are widespread in their distribution, and at least two of these differ markedly within themselves in their role as malaria vectors and possibly in their breeding habits as well. This study has resulted in the delineation of two new subspecies, *Anopheles maculipennis freeborni* Aitken (1939b) and *Anopheles pseudopunctipennis franciscanus* (McCracken) 1904. The recently described *Anopheles boydi* Vargas (1939b) is for the present classified merely as a variant of *Anopheles pseudopunctipennis franciscanus*.

ACKNOWLEDGMENT

Anopheles maculipennis Meigen

Anopheles maculipennis Meigen, 1818, 1:11; Nuttall and Shipley, 1901, 1:45–77, 269–276, 451–
484;; *idem*, 1902, 2:58–84; *idem*, 1903, 3:166–215; Imms, 1907, 7:291; *idem*, 1908, 1:103;
Howard, Dyar, and Knab, 1917, 4:1026; Wesenberg-Lund, 1920; Edwards, 1921, 12:272;
Christophers, 1924, 3:21; Edwards, 1926, 5:268; Freeborn, 1926, 3:448; Dyar, 1928, 452;
Matheson, 1929; La Face, 1929; 8:554; Kumm, 1929, 10:55; Martini, 1930, 40:154; Mont-
chadsky, 1930, 50:560; Vinogradskaia, 1934, 3:378; Hackett and Missiroli, 1935, 14:3; Kis-
sileva, 1936, 5:220; Diemer and van Thiel, 1936, 39:109; Hackett, 1937, 6:1; Stackelberg, 1937,
3:48; Beklemishev and Zhelochovtsev, 1937, 6:819; Marshall, 1938, Hackett, 1938; Weyer,
1939; Bates, 1940; 33:343.
Culex claviger Fabricius, 1805 (nec *Culex claviger* Meigen, 1804, 1:4).
Anopheles selengensis Ludlow, 1920, 27:77.
Anopheles alexandrae-shingarevi Shingarev, 1928, 6:48; Simanin, 1929, 22:503; Tarwid, 1933,
10:57; Zhelochovtsev, 1937, 6:707.
Anopheles maculipennis var. *typicus* Martini, Missiroli, and Hackett, 1931, 35:622.
Anopheles claviger var. *basilei* Falleroni, 1932; Hackett and Missiroli, 1935, 14:51.
Anopheles maculipennis var. *pergusae* Missiroli, 1935, 45:333.
　? var. *fallax* Roubaud, 1934, 27:737; Bates, 1940, 33:343.
　? var. *sicaulti* Roubaud, 1935, 28:107; Bates, 1940, 33:343.
　? var. *subalpinus* Hackett and Lewis, 1935, 14:377; Bates, 1940, 33:343.
　? var. *caucasicus* B. H. ([?]; described by Hackett and Barber, 1935, 4:188, but given no name;
　　see Stackelberg, 1937, 3:48).

Type locality.—Germany (probably Aix-la-Chapelle; see Diemer and van Thiel, 1936, 39:115.
Description.—*Anopheles maculipennis* is a brownish black mosquito. HEAD with tuft of upright
pale scales medianly and black scales laterally; proboscis and palpi dark. THORAX with mesono-
tum having a central pale stripe (pruinose) and dark lateral bands; a rather conspicuous tuft of
pale hairlike scales on anterior margin of mesonotum, and pale golden hairlike scales adorning
central pale stripe; wings with dark scales, forming spots at junction of first (R_1) and second (R_s)
veins, at forks of second (R_{2+3}) and fourth (M_{1+2}) and at cross veins (r m); a pale tache may or
may not be present at wing apex; legs dark brown, apices of femora and tibiae with pale scales.
ABDOMEN brownish black, densely covered with hairs.

DISTRIBUTION

In considering the species as a whole,[1] *A. maculipennis* is Holarctic in distribution.
The area of its occurrence is almost a complete circle, except for a break in eastern
Siberia, where it (*A. maculipennis messeae*) has been found only as far east as
Blagovieschensk on the Amur River, approximately in 128° E. long. and 51° N. lat.
(Maslov, 1936); Feng and Ch'in (1937) have recently recorded it (*A. maculipen-
nis atroparvus?; based on male terminalia) from two localities in Heilungkiang
province, North Manchuria: Lungchen (lat. 48° 44′ N., long. 126° 50′ E.) and
Heiho (lat. 50° 13′ N., long. 127° 27′ E.). According to the Russian authors, Bekle-
mishev and Zhelochovtsev (1937), the northern and southern boundaries of its
range are primarily determined by lack or excess of warmth in summer. *A. macu-
lipennis* is known from scattered localities throughout Siberia and its range dips
farthest south in the west in the Kopet Dagh Mountains of southwestern Turk-
menistan (approximately 38° N. lat., 58° E. long.). Kissileva (1936) records it in
the far north at the Arctic Circle (66° 32′ N. lat.) at Obdorsk on the Ob River
(approximately 67° E. long.).

It is widely distributed in European Russia, being particularly abundant along
the Volga, Dnieper, and Dniester river valleys, along the margins of the Black and
Azov seas, and in the Caucasus. It is widespread throughout Europe, the islands
of the Aegean, and in northern Africa (Morocco and Algeria). To the north, Stack-
elberg (1937) reports it from Lapland (Frey), Kholmogor, somewhat south of
Archangel (Burakova!), and the Solovetskii Islands in the White Sea (Birulia);

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[1] *A. sacharovi* Favr is here considered a distinct species; hence its distribution will not be con-
sidered with that of *A. maculipennis.*
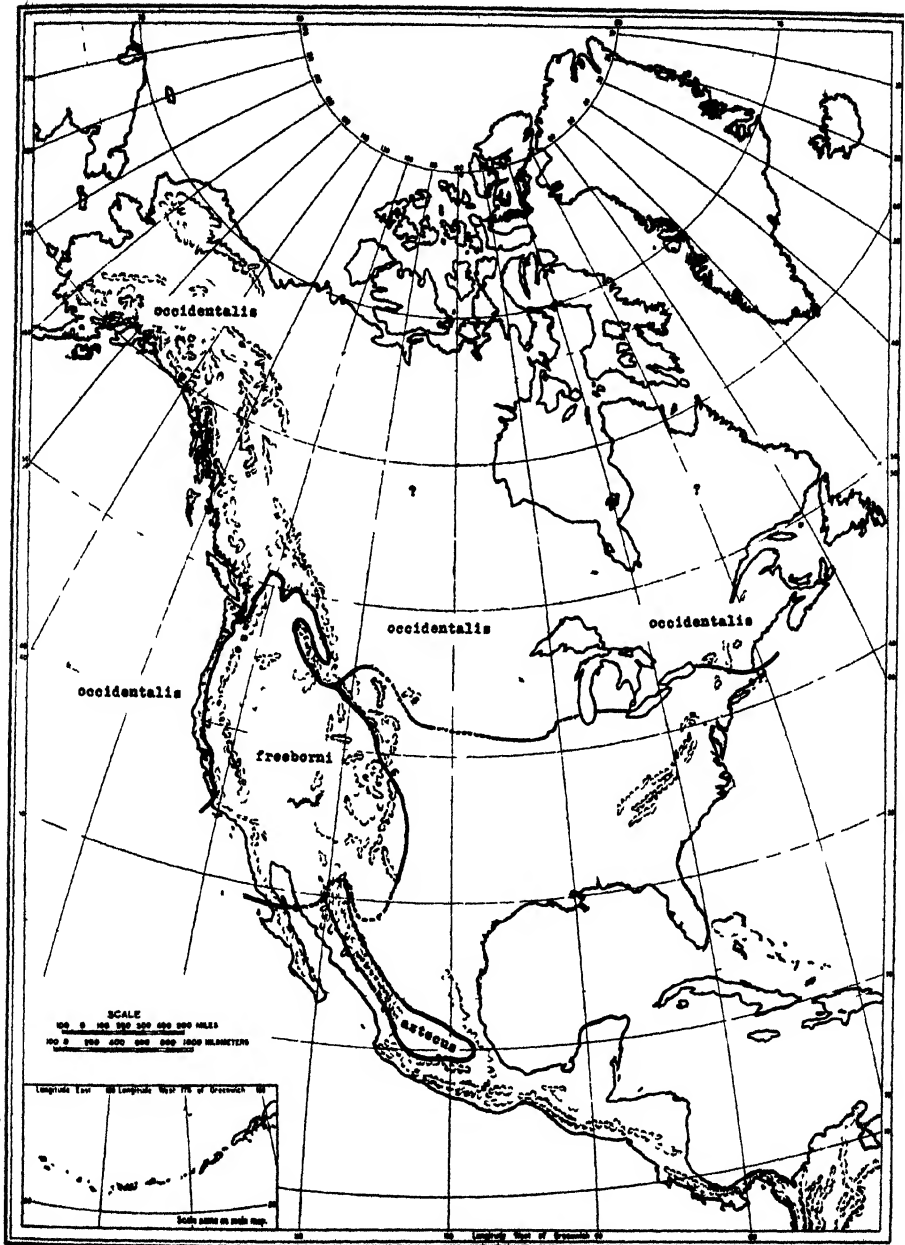
Fig. 1. Distribution of the American *maculipennis* group. Dotted lines indicate doubtful distribution boundary.

he also mentions it from Murmansk (Shingareva), but indicates that the record should be checked; as yet, it is unknown in northeastern European Russia.

In North America *A. maculipennis* occurs primarily in the western United States, west of the Divide (fig. 1). North of southern British Columbia no records are available, because of intervening unexplored country, until the far north is reached,

at Alaska, Yukon and the Canadian Northwest Territories. The most northern record, extending beyond the Arctic Circle, is Owen Bryant's, at Aklavik on the Mackenzie River (69° N. lat, approximately 135° W. long.). The eastward extension of *maculipennis* follows the Canadian border fairly closely, dipping down occasionally into the northern tier of states, appearing on the Atlantic coast in New England as far south as Connecticut; according to available reports, its occurrence in Canada is mainly restricted to the southern regions. It extends along the entire Pacific Slope, and into Baja California for at least half the length of the peninsula. On the continent proper its distribution appears to be discontinuous south of the New Mexico–Arizona border, and it does not reoccur until the central Mexico table-land is reached, where it is to be found in a relatively small area in the states of Guanajuato, Michoacán, Durango, Zacatecas, Jalisco, Puebla, Mexico, and the Distrito Federal (Hoffmann, 1935, 1936; Dampf, 1936; Vargas, 1939a); possibly it ranges south along the Sierra Madre Occidental, but this cannot be definitely stated until further collecting is done in northern Mexico.

SPECIES COMPLEX IN NORTH AMERICA

The history of *Anopheles maculipennis* in North America has been extremely varied, and for many years great confusion existed concerning the exact identity of the species and of the closely related *A. quadrimaculatus* Say of eastern North America. As pointed out by Freeborn (1923), Loew (1864) was probably the first to consider *quadrimaculatus* conspecific with *maculipennis*. Theobald (1901, I:191) included *quadrimaculatus* in the synonymy of *maculipennis*. He states (p. 194) "Say's *quadrimaculata* is the same species as *A. maculipennis*. A large series has been received from E. M. Walker, collected in Canada, which agree in all respects with our European form." Walker's specimens came from DeGrassi Point, Lake Simcoe, Ontario, and may actually have been *maculipennis (occidentalis)*; however, the apical silver wing spot is not mentioned. Later Theobald (1903, III:19) registers doubt about the conspecificity of *maculipennis* and *quadrimaculatus* after seeing Howard's (1900) illustrations of *quadrimaculatus* larvae in which seven pairs of palmate hairs are figured rather than the usual six pairs characteristic of *maculipennis*. Howard, however, had seen Theobald's earlier work, and although listing the American form as *quadrimaculatus*, considered that it must be identical with *maculipennis;* the distribution he gives for this species is definitely that of *quadrimaculatus* as we know it today. Dyar and Knab (1906) separated the two again, but for fifteen or more years thereafter, *quadrimaculatus* continued to appear in the synonymy of the European *maculipennis;* with the appearance of Howard, Dyar, and Knab's (1917) monograph, however, the two species were definitely separated. Herms, in his *Malaria, Cause and Control* (1913), recognized *maculipennis*, as such, as an abundant and widespread species in California.

At the time that Dyar and Knab (1906) distinguished *A. quadrimaculatus* from the European *A. maculipennis*, they established a new species, *A. occidentalis*, for the western form from the Pacific Coast and Canada, based on type material from Stanford University, California. Furthermore, in the discussion of *quadrimaculatus*, Howard *et al.* (1917; p. 1032) stated that Say's type was from the "Northwest Territory," which would make the western form *quadrimaculatus*, sinking *occidentalis*, and the eastern species *A. guttulatus* of Harris (1835). As Freeborn (1923; p. 158) states, "Fortunately before this change became popularized it was pointed out that Say's 'Northwest Territory' was that of 1787, including the area south of the Great Lakes and what is now Minnesota and Wisconsin, and that the expedition on which Say obtained his type penetrated no farther west than the present site

of Pembina, N. D."[3] Finally, Edwards (1921) concluded that *occidentalis* was conspecific with the European *maculipennis* and placed it in synonymy. No demonstrable differences were visible in the larval or adult stage except for the outer claspette spines, which are pointed in *occidentalis* and usually blunt in some of the European *maculipennis*. Eggs were not compared at the time, but at a later date Freeborn furnished Edwards with a description of the egg stage, supposedly of *occidentalis* but actually of *A. maculipennis freeborni* Aitken (1939*b*), which verified his earlier decision (Edwards, 1926). This, however, was before the importance of the eggs of *A. maculipennis* was known. Freeborn (1926), Dyar (1928), and Matheson (1929) have all concurred with Edwards in his interpretation, and until recently this Pacific Coast and Canadian four-spotted anopheline has been classified as *A. maculipennis*. Recently, Aitken (1939*b*), on the basis of morphological, ecological, and distributional characters, split the American and Canadian *maculipennis* into two subspecies, *A. maculipennis occidentalis* and *A. maculipennis freeborni*.

As a result of all this confusion in nomenclature, a number of different names for the same species occur in the literature. This is particularly true of the California writers, and hence one will find that Herms and Freeborn, in particular, refer to all three names, *A. quadrimaculatus, A. occidentalis,* and *A. maculipennis.*

Complications have also arisen in the literature dealing with the Mexican form of *A. maculipennis.* For many years this mosquito of the Mexican "Mesa Central" has been confused with *A. quadrimaculatus; maculipennis* (in the sense of *occidentalis*) apparently was not considered because the silvery apical wing tache was not evident. Howard, Dyar, and Knab (1917; p. 1032), were the first to confuse this form; they included in the distribution of *quadrimaculatus* two records from Valle de Santiago and Salvatierra, Guanajuato, and one record from Maravatio, Michoacán. Dyar (1928; p. 454) added Jaral del Progresso, Guanajuato to this list. All these references have since been shown to pertain to *A. maculipennis aztecus* Hoffmann (1935). Martini (1935) examined material from the Distrito Federal and designated it *A. atropos* on the basis of the narrow, linear wing scales, in spite of the fact that the pale palpal bands characteristic of *atropos* were absent. Dampf (1935*a*) later showed that Martini's specimens were actually *maculipennis*, but in subsequent papers (1935*b*, 1936) he gives reasons for believing the Mexican as well as the American *maculipennis* a distinct species, *A. occidentalis.* Hoffmann (1935), whose paper appeared almost simultaneously with Dampf's (1936), came to the conclusion that the so-called Mexican *"quadrimaculatus"* was actually a form of *maculipennis,* which differed from the California and European forms in the type of egg as well as in the form of the male terminalia; he therefore described it as a new subspecies, *A. maculipennis aztecus.* Vargas (1939*a*) has recently raised *aztecus* to specific status, but his interpretation of *aztecus,* on the basis of morphology and distribution, does not coincide in all respects with mine, as will be explained in the accompanying discussion of the North American subspecies of *maculipennis.*

At the present time I believe that three subspecies of *A. maculipennis* in North America should be recognized: *A. m. occidentalis, A. m. freeborni,* and *A. m. aztecus.*

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[3] As now understood, *occidentalis* is known to occur at Pembina, as well as in various parts of northern and eastern Minnesota and Wisconsin (see Appendix).

Anopheles maculipennis occidentalis (Dyar and Knab)

Anopheles occidentalis Dyar and Knab, 1906, 19:159 (in part); Knab, 1913, 1:36 (in part); Ludlow, 1913 (in part); Herms, 1916a (in part); Dyar, 1917, 5:102; Howard, Dyar, and Knab, 1917, 4:1026 (in part; Fort Gibbon, valley of Mayo, Aweme, Little Current R., Nagagami R., Revelstoke, Portland, Stanford, Ottawa, Weld, Norcross); Dyar, 1918, 6.144 (in part); *idem*, 1919, 7:31; *idem*, 1920, 8:21; Hearle, 1920, 5:115; Dyar, 1921, 13:119; Herms, 1921b (in part); *idem*, 1921c, 14:410 (in part); Root, 1922, 11:390 (in part); *idem*, 1921c, 14:410 (in part); Root, 1922, 11:390 (in part?); Dampf, 1935a, 82:171 (in part; California and British Columbia); *idem*, 1936 (in part; Pacific Coast and Canada); Vargas, 1939a, 19:334 (in part); *idem*, 1939b, 19:362 (in part); Bates, 1940, 33:354 (in part).

Anopheles maculipennis occidentalis, Christophers, 1924, 3:21 (in part); Edwards, 1932 (in part); Hoffmann, 1936b, 2:403 (in part); Stackelberg, 1937, 3:52 (in part); Beklemishev and Zhelochovtsev, 1937, 6:822 (in part); Weyer, 1939 (in part); Aitken, 1939b, 15:191.

Anopheles maculipennis, Theobald, 1901a, 1:193 (in part ?; St. Boniface, Manitoba ?); *idem*, 1903b, 35:211; McCracken, 1904, 15:9; Dyar, 1904, 6:41; Aldrich, 1905, 46:121 (in part); Blanchard, 1905 (in part?); Ludlow, 1906, 69:96 (in part; Benicia Barracks, Presidio, Fort Missoula, Fort Snelling ?); Quayle, 1906, 178:51–53 (in part); Mitchell, 1907 (in part?); Theobald, 1907, 4:26 (in part; California, British Columbia, New Hampshire ?); *idem*, 1910, 5:5 (in part); Herms, 1913 (in part?); Hadwen, 1915, 5:31; Edwards, 1921, 12:272 (in part); Dyar, 1922a, 62:105 (in part; Alaska, Maine); *idem*, 1922b, 10:66 (in part); Matheson and Shannon, 1923, 11:59; Freeborn, 1923, 18:157 (in part); Lenert and Ross, 1923 (in part); Shannon, 1924, 26:142 (British Columbia, Michigan, New York); Edwards, 1926, 5:268 (in part); Twinn, 1926, 58:108; Freeborn, 1926, 3:448; Hearle, 1926; *idem*, 1927, 24:17; Dyar, 1928 (in part); Herms, 1929, 2:710 (in part); Dyar, 1929, 75:8; Matheson, 1929 (in part); Matheson, 1930, 40:154 (in part); Tulloch, 1930, 37:236; Hinman, 1932, 25:614 (in part?); Bull. Calif. Dept. Pub. Health, 1933, 44:13 (in part); Mail, 1934, 288:42 (in part); Tulloch, 1934, 41:206; Johannsen, 1934, 164:46; Hearle, 1934, 5:3355; Hackett, 1937a, 6:7 (in part); Owen, 1937, 126:50; Aitken, 1937 (in part); Lenert, 1939, 65:241 (in part); Lathrop, 1939, 397:828; Irwin, 1941, 52:103.

Anopheles quadrimaculatus, Herms, 1917a, 10:362 (in part); *idem*, 1917b, 13:268 (in part); *idem*, 1919a, 15:8 (in part); *idem*, 1919b, 15:186 (in part); *idem*, 1919c, 34:1586 (in part); *idem*, 1920a, 16:77 (in part); *idem*, 1921a (in part).

Description: female[a]—HEAD with proboscis dark brown, labella somewhat lighter; palpi as long as proboscis, dark brown, with numerous outstanding scales at base, clothed with few straw-colored setae apically; clypeus dark brown, pruinose, bare; antennae brownish black, tori pale brown, a small patch of dull-colored scales medianly; occiput clothed with upright, forked scales, pure white in central patch and black laterally, ocular bristles black, except for clump (including curved white scales) of pure white or "silvery" bristles between eyes. THORAX with mesonotum having pale median stripe (pruinose) bounded laterally by dark bands; distribution of hairlike scales cause median pale stripe to be broken anteriorly into two fairly wide stripes lateral to narrow central dark line which may extend to antescutellar space; median stripe clothed with golden hairlike scales, anteriorly a tuft of pure white linear scales, dark lateral bands partly devoid of long black setae; scutellum pruinose, with marginal row of long and short golden setae; post notum dark brown, pruinose, bare; pleurae pale pruinose with three longitudinal brown stripes; anterior pronotal, proepisternal, spiracular, sternopleural, prealar and upper mesepimeral setae present; coxae pale brown, adorned with golden setae; legs blackish brown, the apices of femora and tibiae with pale scales, tarsal claws simple, 0:0, 0:0, 0:0; wing 4.28 mm., wing scales normally linear, brownish and black, the black particularly evident along costal margin as well as where scales accumulated to form spots at junction of first and second veins, at forks of second and fourth and at cross veins; wing spots smudgy in appearance, a pale tache (frequently pure white) at wing apex; halteres pale brown with blackish knob clothed with dark scales. ABDOMEN dark brown with pruinose areas, the apices of segments darkest, densely clothed with hairs.

Male.—General appearance paler than female. Palpi as long as proboscis, terminal and penultimate segments enlarged; antennal segments pale, the joints dark; wings relatively thin-scaled, except for regions of spots which are very dark and smudgy in appearance; fore-tarsal claw single (fused), toothed, others simple 1:2, 0:0, 0:0. TERMINALIA side pieces (basistyles) slightly less than twice as long as width at base; internal spine just distad of middle; two (very rarely three on one side) stout parabasal spines, the outer one longer and more slender, the inner one shorter, stouter and recurved at tip; claspers (distyles or styles) constricted slightly just beyond middle;

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[a] Description based on specimens from Monterey, California.
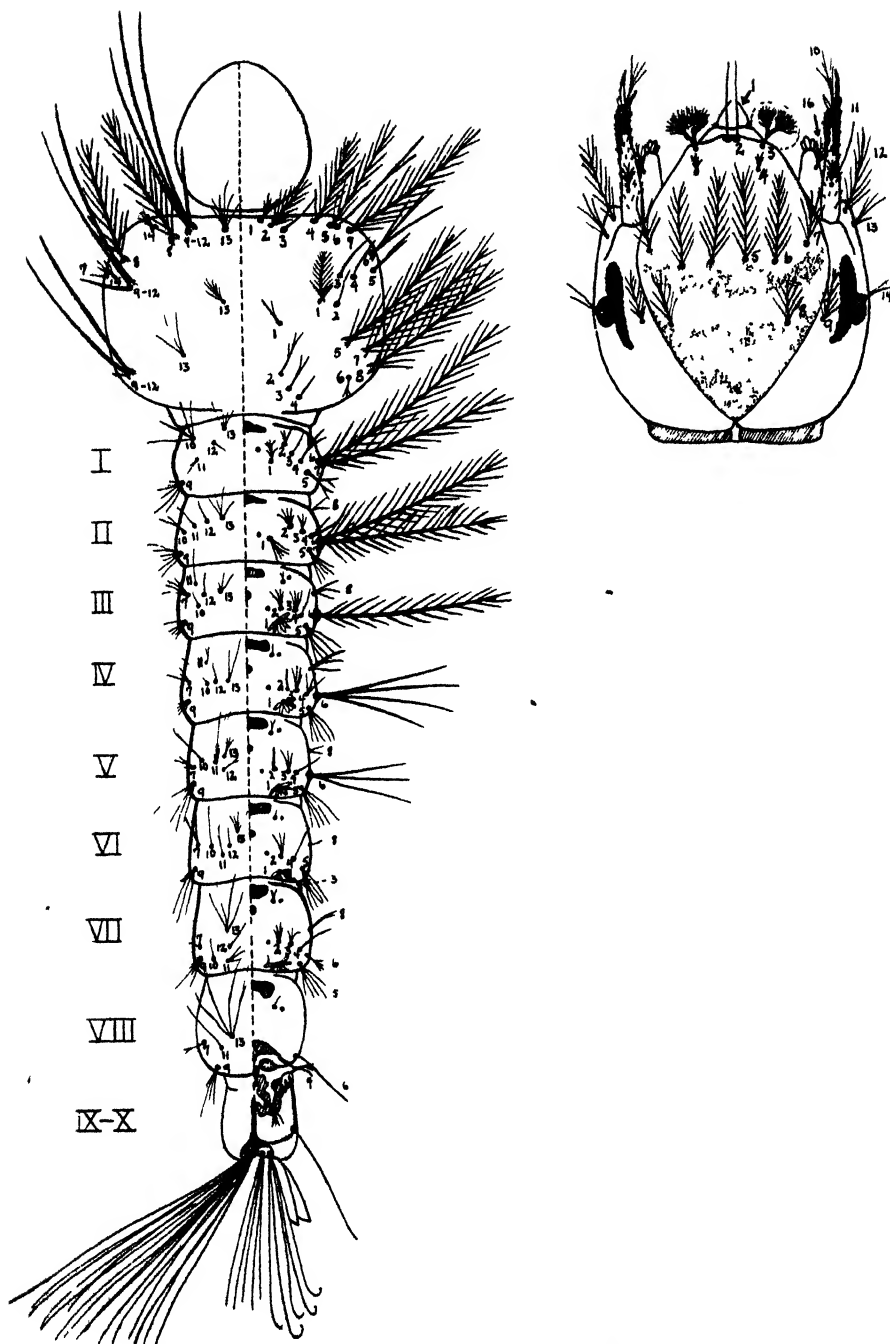
Fig. 2 (left). Larval chaetotaxy of *A. maculipennis occidentalis*
(terminology of Hurlbut, 1938).

rather dense patch of nonpapillated hairs at base of claspers; claspettes bilobed, dorsal[4] (outer) lobe with two rarely one or three; d, z, i hairs of Martini[5] sharp-pointed tapering spines, ventral (inner) lobe with three (occasionally two) sharp-pointed spines (v, s, a hairs of Martini); phallosome with four pairs of nonserrate leaflets, the posterior (apical) pair being the largest; lobe of ninth tergite short, semiacute.

Larva (fig. 2).—HEAD with inner anterior clypeal hairs (no. 2)[6] close together (about half width of papilla, variable), simple, not feathered at tip (except very minutely feathered); outer anterior clypeal hairs (no. 3) dichotomously branched, not longer than extended oral brushes; posterior clypeal hairs (no. 4) short, multiple-branched (about 4–10) near base, slightly mesad of outer clypeal hairs; six frontal hairs (nos. 5, 6, 7) arranged in transverse line between eyes, long and pinnately branched; antennae slightly swollen basally, clothed with short spines except
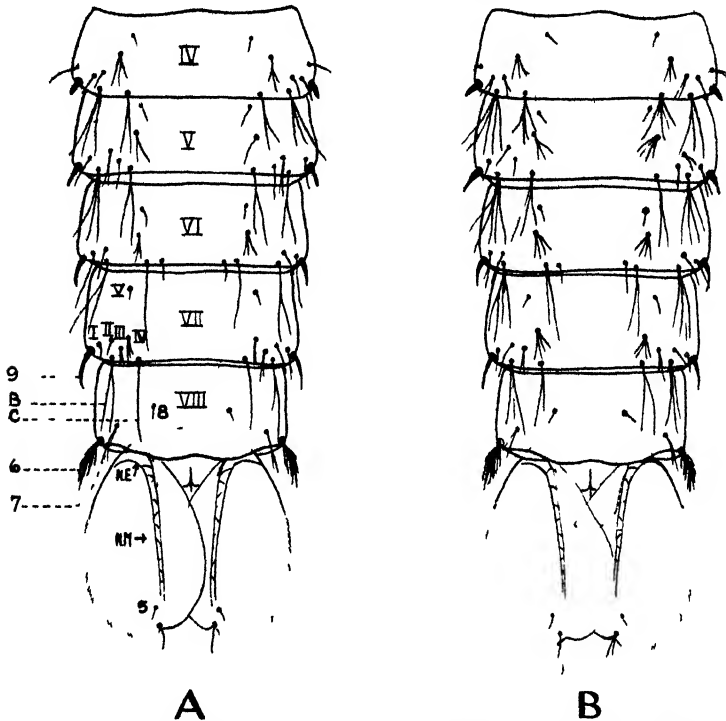
Fig. 3 (right). Pupal chaetotaxy: (A) *A. m. occidentalis;* (B) *A. m. freeborni* (terminology of Senevet, 1930).

outer basal part, apex pigmented, small multiple antennal hair (no. 11) near base (about 10 branches); mental plate with nine teeth; frontoclypeal sclerite with dark transverse band posterior to frontal hairs, followed by pale band, with posterior triangle (posterior to sutural or inner occipital hair no. 8) of sclerite dark; transsutural or outer occipital hair (no. 9) about five-branched. THORAX with anterior submedian prothoracic hairs (nos. 1, 2, 3); 1 is short, split near tip into 1–5 branches, 2 is long, feathered, about 8–10 branches, 3 is short and unbranched (occasionally branched at tip). ABDOMEN with five pairs of palmate (intermediate, partly pigmented); antepalmate hair (no. 2) of segment IV predominantly single (occasionally two- to three-branched, average 1.4), hair 2 of segment V predominantly single (average 1.2 branches); hair 0 on segments II–VI single; lateral plate of segment VIII armed with row of long and short teeth, averaging 20 in number (of which 6 are long).

Pupa[7] (fig. 3).—Segment IV (dorsal): spine 9 short, blunt, hair B four-branched (average

[4] "Primitively dorsal"; before torsion of terminalia.
[5] Terminology of Martini (1933).
[6] Terminology of Hurlbut (1938b).
[7] Terminology of Senevet (1930).

2.9), hair C two- to four-branched (average 2.9); segment V—spine 9 slightly longer, bluntish, hair B one- to four-branched (average 2.37), hair C one- to two-branched (average 1.5); segment VI—spine 9 longer, pointed, hair B one- to three-branched (average 2.14), hair C one- to two-branched (average 1.14); segment VII—spine 9 longest ($\frac{1}{3}$ to $\frac{1}{2}$ length of segment VIII), narrowly pointed, hair B one- to two-branched (average 1.8), hair C single; segment VIII—hair 6 stout, pinnately branched, hair 7 bifurcate, hair 8 single, short, hair V usually single (rarely two-branched); external border of paddle denticulate almost to terminal hair (no. 4), continued as hairs, average length of paddle 878μ, average width 635μ, ratio 1.4:1, hair 4 single (very rarely bifurcate), short, hair 5 single, short.

Egg (No. A–616, Stanford University; fig. 4).—Length 615μ; width inclusive of floats 187.5μ; width between floats 105μ; floats occupy 32–34 per cent of total length, composed of 12 to 14 ribs, smooth; egg considerably pointed at ends, the poles (containing 5 to 8 "end bulbs" resembling a signet ring) protruding somewhat as rounded prominences; marginal frill interrupted by floats; dorsal surface somewhat flatly convex, wide, light gray in appearance, no bands or other marking present except slight darkening at poles, reticulation of dorsal surface coarse, composed of large,

Fig. 4 (left). Egg of *A. maculipennis occidentalis.*
Fig. 5 (right). Wing of *A. maculipennis occidentalis,*
showing pale tache.
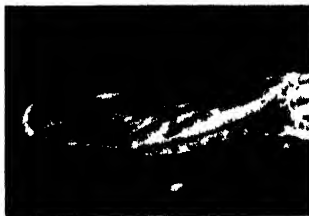
white columellae of irregular, angular form but close together with narrow intervening spaces, columellae tend to form in clumps particularly in middle of egg giving somewhat patchy effect, closer together, smaller, and more rounded at poles, between columellae are small papillae not easily seen; ventral surface composed of columellae without intervening papillae. General appearance—light gray (almost white).

DISCUSSION

The type series of *A. maculipennis occidentalis* (as *A. occidentalis*) as given by Dyar and Knab (1906; p. 159) is as follows: "118 specimens, Stanford University, California (Isabel McCracken); San Diego, Sisson and Thrall, California (Dyar and Caudell); Portland, Oregon (R. P. Currie); Revelstoke, B. C. (H. G. Dyar); Boise, Idaho (J. M. Aldrich); Lehi, Utah (W. A. Hooker). Type—Cat. No. 10, 028, U. S. Nat. Mus."

Mont A. Cazier and Alan Stone have kindly examined for me the type series in the National Museum. It contains 78 specimens of these, 64 are from Stanford University, including the type, which has a distinct "silvery" or pale tache at the wing apex; 45 of them have the light wing tip, 15 do not show the light spot to any extent, and 3 are descaled (fig. 5). Origin of others in the series is as follows: 1 from Thrall, Siskiyou County (no signs of silver tip); 1 from Sisson (now Mt. Shasta City), Siskiyou County, California (no sign of silver tip); 5 from Portland, Oregon (3 without silver tip, 1 with silver tip, and 1 descaled); 1 from Revelstoke,[a] British Columbia (with silver tip); 3 from Boise, Idaho (no sign of silver tip). The silver-tipped wing is thus found only in the more northern coastal forms of this series.

It is quite clear that the type series of Dyar and Knab contained two forms, the silver-tipped *A. maculipennis occidentalis* and the unicolored *A. maculipennis*

[a] In a previous paper (Aitken, 1939b), I included the Revelstoke locality with the unicolored forms, but a reëxamination of the specimen indicates that it is a typical *occidentalis.*

TABLE

MORPHOLOGICAL DISTINCTIONS BETWEEN THE LIFE STAGES OF ANOPHELES AND AMERICAN RACES OF *Anopheles maculipennis*

Adults	Anopheles quadrimaculatus	Anopheles maculipennis occidentalis	Anopheles maculipennis aztecus	Anopheles maculipennis freeborni	New Mexico form
Wing scales	Broad and relatively short; very numerous. Those on apical third of wing almost completely cover membrane (figs. 9, 10)	Intermediate between *quadrimaculatus* and *aztecus*; very dark. Membrane on apical third of wing shows distinctly between veins (fig. 7)	Very narrow and linear; not so numerous as in others. Membrane between veins distinct (figs. 6, 11)	Similar to *occidentalis* but not so dark. Wing membrane distinct (fig. 8)	Similar to *freeborni*
Cubital vein (base)	Composed mainly of broad rounded scales (fig. 15)	Composed of truncate scales, serrated apically	Similar to *occidentalis*	Similar to *occidentalis* (fig. 14)	Similar to *occidentalis*
Wing spots	Distinct (fig. 9)	*Very* distinct (smudgy) (fig. 7)	Indistinct (fig. 6)	Distinct (fig. 8)	Distinct
Wing apex	Unicolorous	"Silver" spot (fig. 5)	Unicolorous	Unicolorous (fig. 16)	Unicolorous
Wing length	5 mm. (Matheson)	4.8 mm.	5.6 mm. (Aitken, 18 specimens) 5-6 mm. (Hoffmann)	4.9 mm.	4.62 mm.
Thorax color	Brown	Dark (blackish)	Frequently reddish brown (almost foxy red); occasionally darker	Brown	Brown
Anterior mesonotal tuft of pale white scales	Well-developed	Well-developed; pure white scales	Small; mainly yellowish scales	Slightly smaller than in *occidentalis*; dirty yellowish white	Similar to *freeborni*

Male terminalia

			Eggs		
External spines (2) of claspette	Blunt and fused apically	Acute	Acute	Acute	Acute
Floats	Smooth. Indented deeply into egg	Smooth. Indented slightly	Rough. Indented into egg	Smooth. Indented slightly	Similar to *freeborn*
Float length	About 35 per cent	35 per cent of total egg length	43 per cent of total egg length (Vargas). 40 per cent (Hoffmann)	35 per cent of total egg length 144–224μ (Herms and Freeborn)	Similar to *freeborn*
No. float chambers	About 24	12–16	17–26 (Vargas) 25 (Hoffmann)	12–16	13–16 (Barber)
Dorsal surface	Gray, no markings	Whitish gray. Columellae close together sometimes clumped, giving patchy effect. No markings (fig. 4)	Dark egg; not gray. Columellae very small and far apart. No markings	Dark gray. Intermediate between *occidentalis* and *aztecus*. Columellae larger than in *aztecus*, but farther apart than in *occidentalis*; no markings (fig. 13)	Apparently similar to *freeborn*

a Immature stages of *A. quadrimaculatus* originating along the Wacissa River Jefferson County, Florida, obtained from the laboratory colony of M. F. Boyd.

TABLE 1—(Continued)

Larvæ

Adults	Anopheles quadrimaculatus[1]	Anopheles maculipennis occidentalis	Anopheles maculipennis aztecus	Anopheles maculipennis freeborni	New Mexico form
Inner clypeal hair	Not feathered at tip. Tubercles separated at least by width of one tubercle	Rarely, if ever, feathered. Tubercles usually not separated by width of one tubercle (fig. 2)	Feathered or simple. Tubercles as in *quadrimaculatus*	Rarely, if ever, feathered. Tubercles as in *occidentalis* (fig. 12)	As in *freeborn*
Post clypeal hair	Usually 2-3 branched near base. (Root)	Multiple tuft near apex		Usually 2-branched near base or middle. Occasionally one or two secondary branches; rarely single	2-branched (7 specimens from Barber)
Frontoclypeal pattern	Posterior triangle without spots except for band between occipital hairs	Pale transverse band just posterior to frontal hairs. Posterior triangle usually dark	Similar to *freeborn* ?	Spotted, rarely banded	Similar to *freeborn*
Hair No. 1. Prothorax	Split apically into 3-4 minute branches (Root)	Split into 2-4 fairly long branches apically		Split into 5-6 long branches along main stem (occasionally apical)	Usually as in *freeborn*
Palmate hair (No. 1)	Segments II-VII	Segments III-VII	Segments III-VII	Segments III-VII	Segments II or III-VII
Hair No. 1. Abd. Seg. 2	Fairly well developed, about 12 leaflets, pigmented (usually) (Root)	Undeveloped	Undeveloped (10-12 branches) (Hoffmann)	Undeveloped	Well developed in 6 of 7 larvæ. Pigmented (usually). (About 12 leaflets)

	Col 1	Col 2	Col 3	Col 4	Col 5
Hair No. 2. Abd. Seg. 4	Usually single, occasionally 2-branched near middle. (Root)	1-3-branched, usually former	1-5-branched. Average 3-branched (Vargas). 7-branched (Hoffmann)	1-4-branched; usually 2-branched	1-3-branched 3-branched.
Hair No. 2. Abd. Seg. 5	Usually single; occasionally 2-branched near middle. (Root)	1-3-branched; usually former	1-4-branched. Average 2-branched (Vargas)	1-3-branched. Usually 2-branched	2-4-branched. Usually 2-branched
Pupa					
Spine No. 9	Blunt, short; those on segment VII about 1/8-1/9 length of segment VIII	Acute, long, those on segment VII 1 3-1/2 length of segment VIII (fig. 3a)		Acute, long; those on segment VII 1, 5-1/3 length of segment VIII (fig. 3b)	Similar to *freeborni?*
Hair B	Segment IV: average 5-branched (3-7): V: 3 (2-4), VI: 3.42 (3-5). VII: 3 (2-3)	Segment IV: 2 9 (2-4), V: 2.37 (1-4), VI: 2.14 (1-3), VII: 1 8 (1-2)		Segment IV: 6.25 (5-8), V: 4.25 (4-5), VI: 4.25 (4-5), VII: 3.6 (3-4)	Similar to *freeborni?*
Hair C	Segment IV: average 5-branched (3-6). V: 2 (2-3), VI: 1.37 (1-2) .VII: 1	Segment IV: 2.9 (2-4), V: 1.5 (1-2), VI: 1 14 (1-2), VII: 1		Segment IV: 5.12 (4-7), V: 4 (2-5), VI: 2 25 (2-3), VII: 1.75 (1-2)	Similar to *freeborni?*

* Immature stages of *A. quadrimaculatus* originating along the Wacissa River, Jefferson County, Florida, obtained from the laboratory colony of M. F. Boyd.

6

7

8

9

Fig. 6. Wing of *A. maculipennis aztecus.* × 17.
Fig. 7. Wing of *A. m. occidentalis.* × 17.
Fig. 8. Wing of *A. m. freeborni.* × 17.
Fig. 9. Wing of *A. quadrimaculatus.* × 17.

freeborni. The presence of two forms at Stanford will be explained later. Appar
ently *occidentalis* and *freeborni* meet on the Columbia River at Portland. Southern
British Columbia and perhaps also Montana are possibly a transition zone and
occidentalis and *freeborni* may occur sporadically throughout this region.

Freeborn (1926, p. 450) writing of *A. maculipennis* Meigen, states, "The dis-
tinctive coppery spot on the wing fringe at the tip is very plain in specimens taken
along the moist coastal strip, but in the central valleys and the foothills of the

Sierra the spot is almost always impossible to distinguish ..." I have examined numerous specimens of *maculipennis* from inland California and have found no trace of a pale tache at the wing apex. See table 1 for a comparison of *A. maculipennis occidentalis* with the other American subspecies of *maculipennis*.

Wing measurements.—Because the Mexico *A. maculipennis aztecus* appears to be a larger mosquito than the American forms of *A. maculipennis*, wing measure-

TABLE 2

WING MEASUREMENTS (mm.) OF FEMALE ANOPHELINES

Wing measurements (mm.)	Number of specimens			
	occidentalis	*freeborni*	*New Mexico (freeborni?)*	*aztecus*
3.5	2	....	....	....
3.6	....	....	....	....
3.7	1	....	....	....
3 8	3	....	....	....
3.9	4	....	....	....
4.0	6	....	....	....
4.1	4	....	1	....
4 2	3	3	4	....
4.3	2	2	...a	....
4.4	2a	3	2	...
4.5	2	8	2	1
4.6	4	7a	1	....
4.7	2	4	....	....
4.8	5	6	....	....
4.9	3	1	....	1
5.0	....	6	....	2
5 1	....	....	....	2
5.2	....	2	....	2a
5.3	....	....	....	1
5.4	....	....	....	5
5.5	....	....	....	...
5 6	....	....	....	....
Average (mm.)	4.28	4.64	4.33	5 2

a Mean wing length.

ments have been made (figs. 6, 7, 8, 9). Table 2 presents the wing measurements of all three subspecies; the New Mexico *maculipennis*, although undoubtedly *A. maculipennis freeborni*, is considered separately because of having certain larval variations which somewhat confuse its positive identification. The method of measurement is that employed by Swellengrebel (see Evans, 1934). It was noted that the specimens of *freeborni* collected in the fall tended to be somewhat larger than spring forms (4.76 mm. as compared with 4.54 mm.).

Male terminalia.—The male terminalia differences in these three subspecies appear to be the least satisfactory of any yet found, but as Martini (1933, p. 86) writes, "The variability of the hypopygium (terminalia) of *A. maculipennis* is too great to allow a clear separation from the most closely related species." Occasionally terminalia preparations of both *A. maculipennis occidentalis* and *A. maculipennis freeborni* may be found which exhibit three parabasal spines on one side and two

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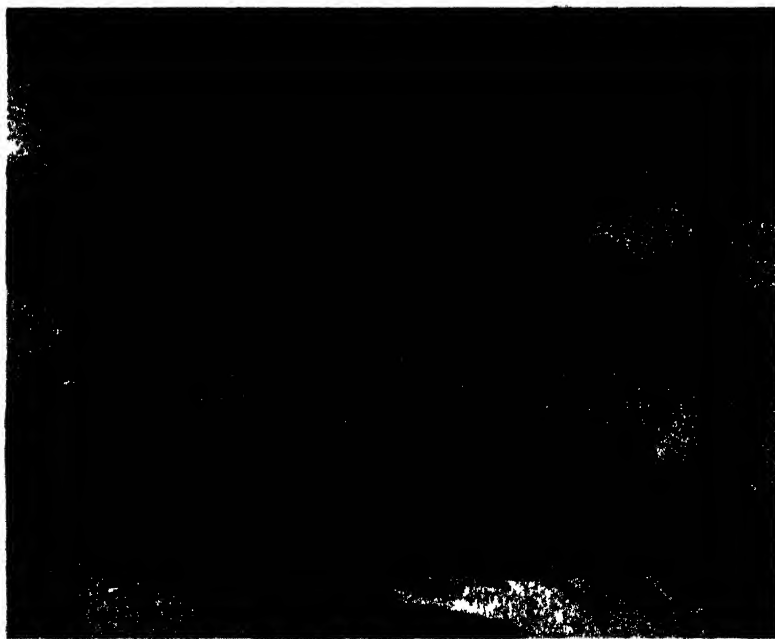
11

Fig 10 Scales on apical third of wing of *A. maçulipennis freeborni.* × 30 ca.
Fig 11. Scales on apical third of wing of *A. maculipennis aztecus.* × 30 ca

on the other. Shingarev (1928) described *A. alexandrae-shingarevi* from Russia separating it from *A. maculipennis,* on the basis of three parabasal spines on the terminalia, but the subsequent observations of Simanin (1929), Tarwid (1933), and Zhelochovtsev (1937), in which two and three parabasal spines were found in the same terminalia preparations, definitely proved the variability of this character.

Larva (fig. 2).—A study of the larval chaetotaxy of *A. maculipennis occidentalis* indicates that this subspecies may be recognized by considering several characters together. Although the anterior inner clypeal hairs (no. 2) are not contiguous, their proximity to each other is such that rarely could another papilla be placed between them. The multiple, basally branched (about 4–10) posterior clypeal hairs (no. 4) are constant and appear to be characteristic of *occidentalis,* quite in contrast to those in *A. maculipennis freeborni* (fig. 12), where hair no. 4 is normally two-branched; rarely is this hair single in *freeborni,* but occasionally there may be one or two secondary branches.

Marshall (1938) has used the head pattern with success in separating the four species of British anophelines. I have found two rather distinct patterns in the California *A. maculipennis* which aid considerably in separating *A. maculipennis occidentalis* (fig. 2b) from *A. maculipennis freeborni* (fig. 12b). Although these patterns vary somewhat and occasionally may verge toward the patterns in the other subspecies, as a rule they are constant for California specimens. The fronto-clypeal sclerite of *occidentalis* is marked by a transverse band of pigment just posterior to, and sometimes including, the frontal hairs; included within this band are the three dark spots characteristic of *maculipennis.* A pale band separates the anterior dark band from the dark posterior triangular area of sclerite (posterior to the inner sutural occipital hair, no. 8) Within this dark posterior triangular area the typical markings of *maculipennis* may be made out in pale forms: a large triangular central spot between the inner sutural occipital hairs (no. 8), an oval spot posterior to hair no. 8, and two oval spots in the apex of the triangle.

Root (1932, p. 779) states, "A few larvae of *A. maculipennis* Mg. (*occidentalis* D. and K.), have the anterior dorsal hair of the prothoracic group (hair I. a. d.) |hair no. 9 of Martini| split. Dr. Martini informs me *in litteris* that this is the rule in the Old World *maculipennis.*" The subspecific identity of the American *A. maculipennis* examined by Root is unknown to me; however, an examination of a great number of larvae of both *A. maculipennis occidentalis* and *A. maculipennis freeborni* has failed to show two branches in prothoracic hair no. 9. If two branches are the rule in European *maculipennis,* the European and American forms would seem different.

The palmate hairs on abdominal segments III–VII are approximately equal in size; those of segment VII may occasionally be slightly smaller; each element is serrate, but is not drawn out into a long point as in *A. pseudopunctipennis.* Table 3 indicates that in *A. maculipennis occidentalis,* the antepalmate hair (no. 2) of abdominal segments IV and V is predominantly single, while it is two- to three-branched in *A. maculipennis freeborni.* According to Vargas (1939a), who examined 52 larval skins of *A. maculipennis aztecus,* hair no. 2 on abdominal segment IV averaged three branches (minimum one, maximum five) and on segment V averaged two (minimum one, maximum four).

The number of long and short teeth on the anal plate, the character originally proposed by Matheson and Shannon (1923) for separating *A. maculipennis* from *A. punctipennis,* has been found too variable to be of value and cannot be used for separating California *punctipennis* from either of the American subspecies of *maculipennis* or these from each other.

Egg (fig. 4).—The egg differences, as presented in the description and in table 1, are not particularly great between *A. maculipennis occidentalis* and *A. maculipennis freeborni* (fig. 13). However, after one has examined several batches from each subspecies, a distinction can be recognized. The effect produced by the size and distribution of the columellae is a light egg in *occidentalis* and a dark egg in *freeborni*. Compared with *A. maculipennis aztecus* these eggs are much more robust and pointed. This robustness is due to the broader and more convex dorsal surface within the marginal frill. The *aztecus* egg is much darker in color, almost black; this effect is produced by the very small and widely separated columellae. Furthermore, the roughened float membrane of the *aztecus* egg is quite in contrast to the smooth floats of the northern subspecies. To my knowledge the eggs of New

TABLE 3

BRANCHING OF HAIR NO. 2 ON ABDOMINAL SEGMENTS IV–V

Species	Segment IV				Segment V			
	Number of branches				Number of branches			
	1	2	3	4	1	2	3	4
freeborni		54	16	3	9	59	2	
New Mexico (*freeborni?*)		2	10	2		6	6	1
occidentalis	22	11	1		27	5	1	

England *occidentalis* have not been examined, but because of the continuous distribution of this subspecies there is no reason to suppose that they would differ from the western forms.

DISTRIBUTION

(See appendix for specific localities; fig. 1)

In California *A. maculipennis occidentalis* extends from Ventura in a narrow strip along the coast almost to the Oregon border (Wonderland Park, Del Norte County, about 18 miles south of Crescent City) ; at present it is known from about forty different localities along the coast. It is found around the margins of the Monterey and San Francisco bays and has spread inland along the valleys; for instance, it has been found at San Juan Bautista at the southern extremity of the Santa Clara Valley, a distance of 47 miles from the southern tip of San Francisco Bay, although San Juan Bautista is only separated from Monterey Bay by about 20 miles, there is a low intervening range of mountains. There are also specimens in the University of California collection from Petaluma and Sebastopol, about 8 and 23 miles, respectively, north of the upper reaches of San Francisco Bay. All of these localities are west of the main body of the Coast Ranges and are subject to the influence of coastal weather; I believe that *occidentalis* will be found well up the Salinas, Santa Clara, Sonoma, and Eel River valleys in California.

There is only one record from Oregon. *A. maculipennis occidentalis* apparently comes up the Columbia River at least as far as Portland, where it was collected by R. P. Currie (Dyar and Knab, 1906). There is also one record from Washington (Lake Watcom, H. G. Dyar). More careful collecting will undoubtedly disclose its presence along both the Oregon and Washington coasts.

The distribution in British Columbia is somewhat confusing, for both *A. maculipennis occidentalis* and *A. maculipennis freeborni* occur in this region, but *occiden-*

talis is the dominant form, since it is known from a number of localities throughout the southern part of the province. Hearle (1927) records both *A. maculipennis* and *A. quadrimaculatus* from British Columbia, which suggests that he was actually dealing with *occidentalis* and *freeborni,* respectively; *quadrimaculatus* was reported from Oliver, Vernon, and Nicola Lake.

A. maculipennis occidentalis has been collected in several localities in Alaska, in Yukon Territory, and in the Northwest Territories, where it reaches its northernmost point in distribution at Aklavik, on the Mackenzie River (69° N. lat.).

The distribution of *A. maculipennis occidentalis* in the greater part of Canada is still unknown. Dyar (1922) does not report its collection by the Canadian Arctic Expedition of 1913–1918, which collected mosquitoes as far east as Coronation Gulf, 110° W. long., 68° N. lat. East of British Columbia the subspecies extends across the continent through southern Canada and the northern areas of the United States; on the Atlantic seaboard, it has been found as far south as Stafford Springs, Tolland County, Connecticut.

Anopheles maculipennis freeborni Aitken

Anopheles maculipennis freeborni Aitken, 1939b, 15:191.
Anopheles maculipennis, Howard, 1901 (in part; Oregon); McCracken, 1904, 15:9 (in part?); Aldrich, 1905, 46:121 (in part); Blanchard, 1905 (in part); Ludlow, 1906, 69:96 (in part); Quayle, 1906, 178:52, 53 (in part); Dyar, 1907, 32:121 (in part); Mitchell, 1907 (in part?); Theobald, 1907, 4:27 (in part; Fort Apache, Arizona, Boise Barracks, Idaho); *idem*, 1910, 5:5 (in part); Herms, 1913 (in part); Edwards, 1921, 12:272 (in part); Dyar, 1922a, 62:105 (in part; California, Nevada, Oregon, Utah); *idem*, 1922b, 10:66 (in part); Freeborn, 1923, 18:157 (in part); Root, 1923, 3:273; Lenert and Ross, 1923 (in part); Shannon, 1924, 26:142 (in part; California); Edwards, 1926, 5:268 (in part); Freeborn, 1926, 3:448 (in part); Hearle, 1926, 17:46 (in part?); Herms, 1926, 21:252; Barber, 1928, 21:738; Dyar, 1928 (in part); Herms, 1929, 2:710 (in part); Barber, Komp, and King, 1929, 44:1300; Matheson, 1929 (in part); Martini, 1930, 40:154 (in part); Gerber, 1931, 15:371; Freeborn, 1932, 16:215; Herms and Frost, 1932, 18:242; Frost, 1932, 18:232; Hinman, 1932, 25:614 (in part); Root, 1932, 15:779 (?); Martini, 1933, 35:65 (in part); Barber and Forbrich, 1933, 48:610; Bull. Calif. Dept. Pub. Health, 1933, 44:13 (in part); Rees, 1934, 10:165; Hackett, 1934, 28:111, 117; Mail, 1934, 288:42 (in part); Herms, Wheeler, and Herms, 1934, 27:995; Herms, 1934, 28:1020; Knowlton and Rowe, 1934, 11:269; Hackett and Missiroli, 1935, 14:13, 14, 37; Stage and Gjullin, 1935, 9:5; Chamberlin and Rees, 1935; Knowlton and Rowe, 1935, 28:824; Greiner, 1936; Knowlton and Rowe, 1936, 13:286; Adams, 1936, 117–372; Hackett, 1937a, 6:7 (in part); Aitken, 1937 (in part); Williams, 1937, 30:21; Hatch, 1938, 1:195; Stage, 1938a; Stage, 1938b; Knowlton, Harmston, and Hardy, 1938, 15:103; Williams, 1938, 2:65; Rees, 1939; Lenert, 1939, 65:241 (in part); Aitken, 1939a, 32:411; Barber, 1939, 19:345; Rees, 1939, 29:6.
Anopheles maculipennis occidentalis, Christophers, 1924, 31:21 (in part); Edwards, 1932 (in part); Hoffmann, 1936b, 2:403 (in part); Stackelberg, 1937, 3:52 (in part); Beklemishev and Zhelochovtsev, 1937, 6:822 (in part); Weyer, 1939 (in part).
Anopheles occidentalis Dyar and Knab, 1906, 19:159 (in part; San Diego, Sisson, Thrall, Portland, Boise, Lehi); Theobald, 1910, 5:85 (in part); Knab, 1913, 1:36 (in part); Ludlow, 1913 (in part); Herms, 1916a (in part); Dyar, 1916, 4:51; Freeborn, 1916, 12:247; Howard, Dyar, and Knab, 1917, 4:1026 (in part); Freeborn, 1917a, 10:355; *idem*, 1917b, Oct.; Dyar, 1918, 6:144 (in part); Freeborn, 1920, 15:281; Herms, 1921a (in part); Herms, 1921c, 14:410 (in part); Freeborn, 1921, 14:415; Root, 1922, 11:390 (in part); Purdy, 1925, 145:2, 32; de Buck, Schoute, and Swellengrebel, 1930, 9:101; Dampf, 1935a, 82:171 (in part); *idem*, 1936, 18:91 (in part); Vargas, 1939a, 19:334 (in part); *idem*, 1939b, 19:362 (in part); Bates, 1940, 33:354 (in part).
Anopheles quadrimaculatus, Herms, 1915, 13:185; *idem*, 1916b, 11:16; *idem*, 1917a, 10:362 (in part); *idem*, 1917b, 13:268 (in part); Howard, Dyar, and Knab, 1917, 4:1032 (in part; Colorado, Utah); Cockerell, 1918, 11:198; Herms, 1919a, 15:8 (in part); *idem*, 1919b, 15:186 (in part); *idem*, 1919c, 34:1586 (in part); *idem*, 1920b, 15:211; *idem*, 1920a, 16:77 (in part); *idem*, 1920c, 35:276; Herms and Freeborn, 1920, 7:69; Purdy, 1920, 16:79; Herms, 1921b (in part); Dyar, 1924, 12:41; Hearle, 1927, 24:17 (?); Walker, 1930, 62:150; Geiger and Gray, 1931, 46:517.
Anopheles aztecus, Hoffmann, 1936b, 2:403 (in part; southwestern United States); Vargas, 1939a, 19:338 (in part; Estados de California y Nuevo Méjico, E. U.); *idem*, 1939b, 19:362 (only the name, not the egg).

Description: female.[9]—Similar to *A. maculipennis occidentalis*, but lighter in general appearance. HEAD with occiput clothed with upright, forked scales, dull yellowish white in central patch and black laterally, ocular bristles black, except for clump, which includes a few dull yellowish white scales, of golden bristles between eyes. THORAX with mesonotum having less contrasting pale median stripe and lateral bands, anterior margin of mesonotum with tuft of dull yellowish white linear scales, thoracic integument less melanic than in *occidentalis;* wing 4.64 mm., spots smaller, less pronounced, scales unicolorous, pale tache at wing apex absent (see fig. 16).

Males.—Wing spots weakly defined. Terminalia similar to *A. maculipennis occidentalis;* patch of nonpapillated hairs at base of claspers reduced, less pronounced; lobe of ninth tergite long, slender, and acute.

Larva (fig. 12).—HEAD with inner anterior clypeal hairs (no. 2) close together, similar to *A. maculipennis occidentalis*, very rarely feathered at tip; posterior clypeal hairs (no. 4) fairly long, usually two-branched near base or middle, occasionally one or two secondary branches, rarely

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[9] Description based on specimens from Davis, California.
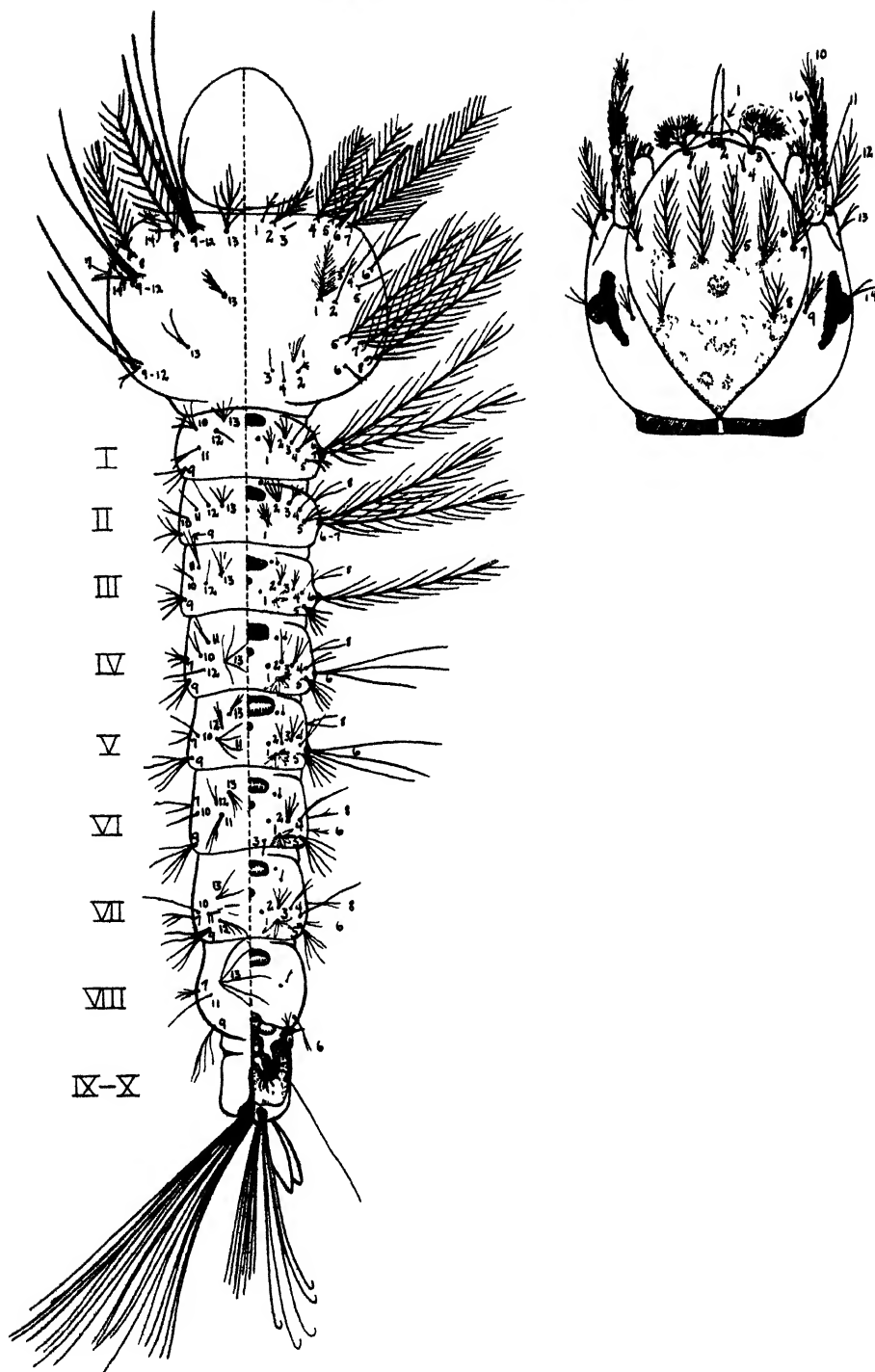
Fig. 12. Larval chaetotaxy of *A. maculipennis freeborni*
(terminology of Hurlbut, 1938).

single; antennal hair (no. 11) variable, about 4–7 branches; frontoclypeal sclerite with three well-defined spots just posterior to frontal hairs, followed by pale area, with posterior triangle composed of one large triangular central spot between sutural or inner occipital hairs (no. 8), an oval spot just posterior to hair 8 and two oval spots in apex of triangle, occasionally posterior triangular area completely dark but with pale center. ABDOMEN with hair 1 on segment II not true palmate, partly developed, antepalmate hair (no. 2) of segment IV one- to four-branched (average 2.8), hair 2 of segment V one- to three-branched (average 1.9).

Pupa (fig. 8*b*).—Segment IV (dorsal)—spine 9 short, blunt, hair B five- to eight-branched (average 6.25), hair C four- to seven-branched (average 5.12); segment V—spine 9 slightly longer, enlarged base produced into dull point, hair B four- to five-branched (average 4.25), hair C two- to five-branched (average 4.0); segment VI—spine 9 longer, hair B four- to five-branched (average 4.25), hair C two- to three-branched (average 2.25); segment VII—spine 9 longest (⅕ to ⅓

Fig. 13. Egg of *A. maculipennis freeborni*.

length of segment VIII), pointed, hair B three- to four-branched (average 3.6), hair C one- to two-branched (average 1.75); segment VIII—hair 6 stout, pinnately branched, hair 7 bifurcate, hair 8 single, short, hair V usually single (rarely two-branched); paddle, average length, 973μ, average width 690μ, ratio 1.4:1, hair 4 short, sinuate, frequently bifurcate, hair 5 single.

Egg (no. A–379, La Grange, Stanislaus County; fig. 13).—Length 625μ; width inclusive of floats 200μ; width between floats 112μ; floats occupy 30–40 per cent of total length, composed of 12 to 16 (average 14) ribs, smooth; egg distinctly pointed at ends, the poles protruding somewhat as rounded prominences; marginal frill interrupted by floats; dorsal surface somewhat shallowly convex, wide, dull gray (darker than *A. maculipennis occidentalis*), no bands or other markings present except darkening at poles, reticulation of dorsal surface not so coarse as in *occidentalis*, columellae tend to be more uniformly shaped, somewhat more rounded and smaller in size and more evenly dispersed over the dorsal surface with relatively wide intervening dark spaces, the intervening papillae much more prominent than in *occidentalis*, easily seen with 12.5 × ocular and 6.8 × objective; ventral surface as in *occidentalis*. General appearance, gray.

DISCUSSION

Dyar and Knab's type series of *"A. occidentalis"* contained specimens of the form now known as *A. maculipennis freeborni;* in that series the following localities pertain to this subspecies: San Diego, Sisson (Mt. Shasta City), Thrall, and Stanford University (possibly the fifteen unicolorous forms); Portland, Oregon (three specimens); Boise, Idaho (three specimens); and Lehi, Utah (three specimens). Except for San Diego and Portland, all these localities are inland. This form with unicolorous wings, in contrast to the silver-tipped *A. maculipennis occidentalis*, is the so-called inland subspecies, which, as will be seen shortly, only reaches the ocean south of San Luis Obispo, California.

Practically all of the literature pertaining to the North American *A. maculipennis,* excluding that concerning the eastern *A. quadrimaculatus* when it was considered conspecific with *maculipennis,* deals with the subspecies *A. maculipennis freeborni.* For instance, in California, where *A. maculipennis occidentalis* exists only in a narrow strip along the coast, very little mention of the coastal forms was made by Herms. He was primarily interested in the anophelines of the interior valleys where malaria existed. An example of the confusion existing in the literature may be found in the following quotation from one of the early papers of Herms (1919c, p. 1587), "In this report *Anopheles occidentalis* (Dyar and Knab) has been included with *A. quadrimaculatus,* and for the purpose of this paper is simply regarded as a variety of the latter. It is interesting in this connection to note that in the vast majority of *A. quadrimaculatus* collected in California no differences were detected when compared with eastern specimens, many of which the writer collected during the summer of 1918. It is agreed, however, that specimens corresponding more or less perfectly with the descriptions of *A. occidentalis* have been collected in California, particularly in the coastal counties and here and there in other parts of the state. This is, apparently, a melanotic variety of *A. quadrimaculatus,* a matter with which this report, however, has no immediate concern." Actually, in that report only the north coastal counties specimens were referable to *occidentalis,* the remainder being *freeborni.*

It is evident from this that anyone using any of the existing keys to the anopheline mosquitoes of the United States and Canada would only be able to separate *A. quadrimaculatus* adults, exclusive of terminalia, from *A. maculipennis (occidentalis)* occurring along the northwestern coastlines of the United States and Canada as well as the regions adjoining the international boundary and in New England. This similarity in the adults of *A. quadrimaculatus* and *A. maculipennis freeborni* accounts for the confusion that has crept into the literature pertaining to the two mosquitoes. However, after having compared *A. quadrimaculatus* with *A. maculipennis freeborni,* I am inclined to believe, even though the male terminalia preparations are not available, that the former may be distinguished from *freeborni* by the type of scales on the outer third of the wing, these being broader and hence more obtusely pointed, as well as more numerous and more evenly laid down (fig. 9). In contrast, on the wing of *freeborni* these scales are narrower and thus more acutely pointed and are less numerous; instead of being laid down evenly and pointing in the direction of the vein, many of them project out in various directions, giving the wing a somewhat disorderly appearance (fig. 8). Because of the regular manner in which the scales of the apical third of the wing are laid down in *quadrimaculatus,* the wing membrane is almost entirely covered between veins, whereas, in *freeborni* as in *occidentalis,* there are rather conspicuous longitudinal bare spaces between the veins. In *freeborni* the scales of the basal part of the cubitus (5th longitudinal vein) as far as the fork are distinctly truncate at their apices with serrate edges (fig. 14), whereas in *quadrimaculatus* they are predominantly broadly rounded without serrate edges (fig. 15). For differential characters see table 1.

Larva (fig. 12).—In the larval head of *A. maculipennis freeborni,* postclypeal hair no. 4 is fairly long and normally is two-branched between the base and the middle; rarely this hair may be single; infrequently it may have one or two secondary branches. The marking of the frontoclypeal sclerite (fig 12b) is similar to that of *A. maculipennis occidentalis,* but the intervening ground pigmentation between the spots is present only rarely, and then the posterior triangular area has a pale center. This type of marking gives the head a more spotted appearance than in *A. maculipennis occidentalis.* For additional characters, see tables 1 and 3.

Egg (fig. 13) —The eggs of *A. maculipennis freeborni* have previously been described by Herms and Freeborn (1920), who obtained their material from Vina, Tehama County and by Herms and Frost (1932) who obtained theirs at Robbins,

14
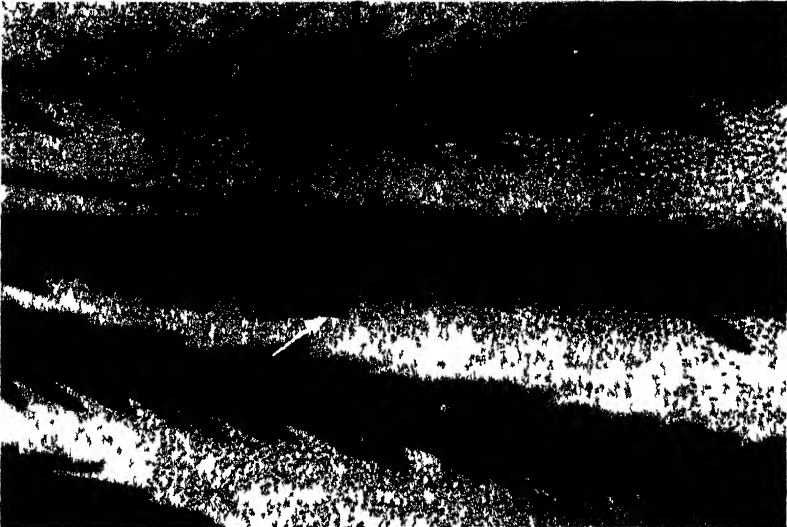
15

Fig 14. Scales of the cubitus on the basal part of the wing of
A. maculipennis freeborni × 30 ca.
Fig 15. Scales of the cubitus on the basal part of the wing of
A. quadrimaculatus. × 30 ca.

Sutter County; both localities are in the Sacramento Valley. Since the character of the float membrane is important in separating the European forms of *maculipennis,* it was examined in the American subspecies, and found to be smooth in both *freeborni* and *occidentalis.*

New Mexico subspecies.—The most noteworthy regional variation so far found occurs in larvae from Leasburg, Doña Ana County, New Mexico, collected September 19, 1931, and furnished through the kindness of M. A. Barber. Six out of twelve larvae examined have a well-developed palmate hair (no. 1) on abdominal segment II (about 14 elements), in this respect resembling *A. quadrimaculatus* and occasional specimens of *A. punctipennis;* in the others this hair is intermediate in form or entirely nonpalmate in character. An examination of other characters disclosed the following: (1) The inner anterior clypeal hairs (no. 2) are close together as in *A. maculipennis freeborni* and, but for one exception which was two-branched, are nonfeathered at tip. (2) The posterior clypeal hair (no. 4) is two-branched near the base, as in *freeborni*, and rarely has one, or up to four, branches. (3) Hair no. 2 abdominal segments IV and V is three-branched, as in *freeborni*, rarely two- to four-branched. These larvae were identified by Barber as *A. maculipennis;* they may be *A. punctipennis*, a species which I have great difficulty in separating from *maculipennis* in the larval stage. Bradley (1936*b*) recognized *punctipennis* by hair
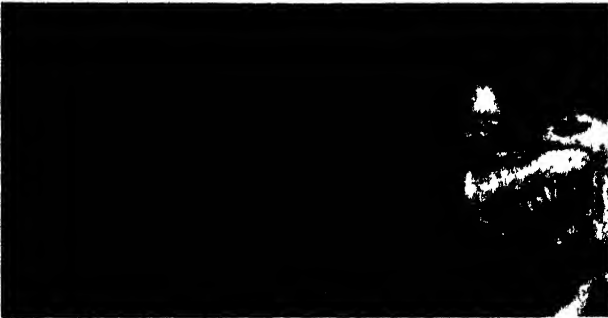
Fig. 16. Wing of *A. maculipennis freeborni*, showing absence of pale tache characteristic of *A. maculipennis occidentalis*. Slightly pale tip is due to unavoidable light reflection.

no. 2 on abdominal segments IV and V, which usually has two branches (rarely one or three), and the posterior clypeal hairs (no. 4) have two branches near the base; but in the West these characters are unsatisfactory, as can be seen from the description of the larva of *freeborni*. Furthermore, Barber and Forbrich (1933), whose report is based in part on the same material, do not record *punctipennis* from Doña Ana County nor the entire New Mexico section of the Rio Grande. Since the adults collected in the same region are typical *freeborni,* and not *quadrimaculatus,* I temporarily consider these New Mexico larvae as merely aberrations of *freeborni.*

DISTRIBUTION
(Fig. 1)

A. maculipennis freeborni occurs in general throughout North America west of the Rocky Mountains. Its distribution extends a short distance into southern British Columbia (Vernon) in the Okanagan Valley. If it occurs outside of the Okanagan Valley, where the climate resembles that found in the Great Basin, it apparently overlaps *A. maculipennis occidentalis,* and southern British Columbia can be considered a transition zone for these subspecies. The distribution of *freeborni* in Montana is likewise confusing. I have seen specimens of this mosquito, through the courtesy of C. B. Philip, from Hamilton and other points in the upper reaches of the Bitter Root Valley, which suggests that it may have migrated from the Great Basin areas of Idaho and Washington into Montana by way of the Bitter Root

River. There are a few records of *freeborni* from southern Idaho (Boise, Boise Barracks, Fish Haven), but elsewhere in the state little is known of the anopheline fauna.

So far as I am aware, nothing is known of the anopheline fauna of western Wyoming; however, *A. maculipennis freeborni* presumably exists in this region. Very few records also are available from Colorado. Cockerell (1918) reports *A. quadrimaculatus* from Hotchkiss and Delta, Delta County, in the western part of the state. Walker (1930) also reports *quadrimaculatus* from the western border at Appleton, Mesa County; this identification was based on three females and seven larvae. As has been pointed out, the task of separating females of *freeborni* from *quadrimaculatus* is not easy; unfortunately, no males were available to clinch the diagnosis. Furthermore, the identification of larvae is generally a difficult matter; at the time that this note appeared, *quadrimaculatus* was separated from *A. maculipennis* on the basis of six pairs of palmate hairs (no. 1) in the former and five pairs in the latter (Dyar, 1928; Matheson, 1929). No description of the larva appears with this note, so that one is at a loss to know what was the condition of the palmate hairs, the inner clypeal hairs, and other important characters. If the palmate hairs are constant in number, this should be a good character, but some of the specimens of *maculipennis* (*freeborni?*) from New Mexico, previously referred to, have six pairs of palmate hairs. Recently C. R. Walker furnished me with male and female specimens from Delta, Colorado, collected in August, 1932. The outer claspette lobes of the terminalia are furnished with the sharp-pointed spines characteristic of *freeborni;* the wing scales of the female, as described previously, are typical of this mosquito. Hence it appears that the published Colorado records above should be credited to *freeborni* and not to *quadrimaculatus* or, as Hoffmann (1936b) believed, to *A. maculipennis aztecus*. It is my belief that *quadrimaculatus* does not exist west of the Rocky Mountains; it may possibly occur in New Mexico, particularly in the Rio Grande, Pecos, and Canadian river valleys, but as yet it has not been reported from that state.

Through the investigations of Barber and others *A. maculipennis* (*freeborni*) is known to occur rather widely in the irrigated regions of New Mexico, particularly in the north along the San Juan and Rio Grande rivers; although present farther south, *A. pseudopunctipennis* appears to be the predominant anopheline in the lower section of the state. Recently *maculipennis* (*freeborni*) has been found in the Pecos Valley in the southeastern corner of New Mexico. (Barber, 1939). Through the kindness of M. A. Barber, I had an opportunity to examine *maculipennis* material from New Mexico and found the adults to be typical *A. maculipennis freeborni:* no specimens with the characteristic long wings and narrowly linear wing scales of *A. maculipennis aztecus* were found. As has been noted previously, a few of the larvae presented characters intermediate between *A. quadrimaculatus* and *freeborni;* the majority, however, were typical of the latter mosquito (see table 3).

Barber, Komp, and King (1929) were unsuccessful in finding *A. maculipennis* (*freeborni*) in Texas, their surveys having been made along the Rio Grande in Cameron, Hidalgo, Webb, Val Verde, and El Paso counties. They suggest, however, that "it may be expected there, at least in the cooler waters of the mountain regions." Barber and Forbrich (1933, p. 614) state: "Differences in elevation, character of water, and temperature of the river valley above and below El Paso are not great, but it may be that the city marks the southern limit of *A. maculipennis*, at least of its occurrence in large numbers." Recent correspondence with C. P. Coogle discloses that *maculipennis* (*freeborni*) occurs throughout the western tip of Texas chiefly in the region included between El Paso, Val Verde, and Gaines

counties. Barber and Forbrich were unable to find *A. quadrimaculatus* in New Mexico although it is present in the lower Rio Grande Valley of Texas.

I now know of only two records of *A. maculipennis* from Arizona, both of which are in the southern part of the state (San Bernardino Ranch, near Douglas, Cochise County, Aug., F. H. Snow, 3,750 feet; Arivaca, Pima County, Dec. 5, 1932, Marx). The Cochise County specimens, two females from the Stanford University Collection, are typical *A. maculipennis freeborni;* the Arivaca specimen, in the U. S. National Museum, has been identified as *freeborni* by Alan Stone.

The known distribution of *A. maculipennis freeborni* in Nevada is restricted to a few localities in the Reno region. Washington (Hatch, 1938) and Oregon (Stage and Gjullin, 1935, Stage, 1938a) both report the presence of *A. maculipennis (freeborni)* ; it is particularly abundant between the Cascades and the Coast Ranges. I examined material from these three states and found it to be typical *freeborni.* According to Stage and Gjullin (1935) *A. punctipennis* appears to be the more common anopheline in Oregon.

A. maculipennis freeborni reaches its peak of development in California, where it has been found widely throughout the state (Herms, 1919a, c, 1920b, c, 1928, Freeborn, 1926, Aitken, 1937) except along the north coast, being particularly abundant in the Sacramento and San Joaquin valleys; it reaches the coast in southern California, from San Luis Obispo southward. It apparently does not occur in the drier regions east of the southern Sierra except in Owens Valley (Aitken, 1939a), and it has never been collected in the hot Coachella and Imperial valleys of the southeastern corner of the state. As in New Mexico, *freeborni,* although fairly common in southern California, gives way to *A. pseudopunctipennis* as the dominant anopheline of this region.

A. maculipennis freeborni quite probably occurs in the north central plateau adjoining southern New Mexico. At least we know of its presence in Baja California, for I have had the opportunity of examining adult specimens of typical *freeborni* from this region collected by A. E. Michelbacher and E. S. Ross in 1938 (Distrito del Norte: Santo Tomás, Aug. 3, and San Fernando Mission, Aug. 1).

Anopheles maculipennis aztecus Hoffmann

Anopheles maculipennis aztecus Hoffmann, 1935, 6:3; *idem*, 1936a, 7:310; *idem*, 1936b, 2:403 (in part; Mexico); *idem*, 1936c, 2:370; Ripstein, 1936 (not seen); Hackett, 1937a, 6:8 (in part; Mexico); Beklemishev and Zhelochovtsev, 1937, 6:822; Weyer, 1939; Aitken, 1939, 15:191.

Anopheles aztecus, Vargas, 1939a, 19:334 (Mexico); *idem*, 1939b, 19:362 (not in California); Bates, 1940, 33:354.

Anopheles maculipennis, Dampf, 1935b, 16:2.

Anopheles occidentalis, Dampf, 1935a, 82:171 (in part; Mexico); *idem*, 1936, 18:91 (in part; Mexico).

Anopheles quadrimaculatus, Howard, Dyar, and Knab, 1917, 4:1032 (in part; Guanajuato); Hoffmann, 1927, 26:187 (in part; "Mesa Central"); Dyar, 1928 (in part; Guanajuato); Hoffmann, 1929, 2:11 (not seen); Ancona, 1930, 1:33; Hoffmann, 1931, 25:523 (in part; central plateau); Bustamente, 1935, 12:86, 87 (in part; central plateau).

Anopheles atropos, Martini, 1935, 1:19.

Description; female.[10]—HEAD with proboscis dark brown, labella with few palish hairs at tip; palpi as long as proboscis, dark brown, with numerous outstanding scales at base; clypeus dark brown, pruinose, bare; antennae brownish black, tori dark brown, a small patch of dull-colored scales medianly; occiput clothed with upright forked scales, dull grayish white in central patch and black laterally, ocular bristles black, except for clump, which includes curved dull grayish white scales, of golden bristles between the eyes. THORAX with mesonotum light coffee-colored, almost russet, with palish pruinose median stripe bounded laterally by coffee-brown bands but the demarcation not distinct, median stripe broken up by three longitudinal lines and clothed with short golden hairlike scales, anterior margin of mesonotum with small tuft of yellow hairs (paler than the rest), brown lateral bands partly devoid of long black setae; scutellum pale brown, pruinose; anterior pronotal, proepisternal, spiracular, sternopleural, prealar, and upper mesepimeral setae present; coxae pale brown, adorned with golden setae; legs brown, the apices of femora and tibiae with pale scales, tarsal claws simple, 0:0, 0:0, 0:0; wing 5.2 mm., wing scales narrowly linear, sparse (similar to *A. atropos*), brown, accumulated to form spots at junction of first and second veins, at forks of second and fourth and at cross veins; wing spots indistinct (much less distinct than in *A. maculipennis freeborni*), scales unicolorous, no pale tache at wing apex; halteres pale brown with blackish knob clothed with dark scales. ABDOMEN dark brown with pruinose areas, the apices of segments densely clothed with golden hairs.

Male.—Wing spots very weakly defined. *Terminalia* similar to *A. maculipennis occidentalis* and *A. maculipennis freeborni.*

Larva (based on description by Hoffmann, 1935; Vargas, 1939).—HEAD with papillae of inner anterior clypeal hairs (no. 3) separated by at least width of one of these papillae, single or feathered with two to three branches apically; posterior clypeal hairs (no. 4) short and without apical branches; antennal hair (no. 11) with 7 branches; mental plate of nine teeth; frontoclypeal sclerite markings apparently similar to *A. maculipennis freeborni.* THORAX with anterior sub median prothoracic hairs (nos. 1, 2, 3) as follows: 1 is short (slightly longer than 3), split apically into 1–8 branches, 2 with five branches, 3 is short and unbranched. ABDOMEN with five pairs of approximately equal hairs (no. 1) on segments III–VII, composed of 20 to 22 nonserrate, pointed elements; hair 1 on segment II not palmate, composed of 10 to 12 branches arising at intervals from stem; antepalmate hair (no. 2) of segment IV one- to five-branched (average 3), hair 2 of segment V one- to four-branched (average 2); lateral plate of segment VIII armed with about 27 teeth (about 8 long).

Pupa.—Undescribed.

Egg.[11]—Length 550–587.5μ (average 566.2μ); width inclusive of floats 187.5μ; width between floats 75μ; floats occupy 42 to 47 per cent (average 45 per cent) of total length, composed of 17 to 26 ribs, intercostal membrane sporadically rough, all areas of membrane not rugose to same degree, parts of it may be smooth; egg quite rounded at poles giving a somewhat blunt appearance; marginal frill interrupted by floats, but float membrane contiguous with dorsal surface is flattened in a narrow strip giving effect of a continuation of marginal frill; dorsal surface almost flat, narrow, dark in appearance, no bands or other markings present, reticulation of dorsal surface delicate, composed of very small, dull gray columellae distributed uniformly, with wide intervening dark spaces, minute papillae scattered among columellae; ventral surface finely granular, composed of columellae but not papillae. General appearance dark gray, blackish.

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[10] Description based on specimens from Tulyehualco, D. F., Mexico, October, 1939 (L. Vargas).

[11] Description based in part on material received from Mexico through L. Vargas (June 8, 1939).

DISCUSSION

Male terminalia.—There appears to be some doubt concerning the distinctiveness of the male terminalia of *A. maculipennis aztecus*. I have seen no preparations of the terminalia, and therefore used descriptions by the Mexican investigators.

In his original description of *A. maculipennis aztecus*, Hoffmann (1935, p. 15) states, "Las cerdas de la claspeta de *maculipennis aztecus* son distintas de las de la forma californiana de la costa. (Conf. Freeborn, 1929, Pág. 449.) En comparación con las formas europeas de las especie, se parecen en su arreglo general más a la forma típica, pero con la marcada diferencia de que las dos cerdas exteriores siempre presenten bien definidas puntas agudas, y no puntas romas como en *maculipennis typicus*. El grupo medio consta en todos nuestros ejemplares de una sola cerda gruesa y puntiaguda, del mismo grueso que las cerdas exteriores o un poco más delgada; la cerda interior es larga y delgada.

"En los detalles del arreglo se notan pequeñas diferencias que presento en las figuras ... ."

I have compared male terminalia preparations of both *A. maculipennis occidentalis* and *A. maculipennis freeborni* with the description and figures of *A. maculipennis aztecus* and can find no significant difference as suggested by Hoffmann. No mention was made by that author of the presence of the nonpapillated hairs at the base of the claspers or the form of the lobe of the ninth tergite.

Dampf (1936) has made a rather comprehensive group study of *A. maculipennis* male terminalia, examining material of *maculipennis* (*occidentalis*) from Michigan, *maculipennis* (*freeborni?*) from Osoyoos and Oliver both in the Okanagan Valley, British Columbia and from Española, New Mexico, and the Sacramento Valley, California. He also examined "*A. occidentalis*" (*aztecus*) from Peñón Viejo, D. F., Mexico, *A. maculipennis labranchiae*, *A. maculipennis messeae*, and *A. maculipennis maculipennis* from Rome, Italy, and *A. quadrimaculatus* from Houston, Texas. He found that the lobes of the ninth tergite were similarly slender and conical in specimens from British Columbia, California, and Mexico. The British Columbia specimens, coming from the Okanagan Valley, undoubtedly are *A. maculipennis freeborni*, as are those from California; hence, it appears that these structures are very similar, if not identical, in *A. maculipennis freeborni* and *A. maculipennis aztecus*. The Michigan specimens, as we know, were *A. maculipennis occidentalis*, and Dampf found the ninth tergite lobes to be quite different; they were larger, the apices were much wider than the bases and some were sharppointed. Dampf went so far as to suggest that the Michigan specimens might belong to a different geographical variety. The lobes of the ninth tergite in the California *occidentalis*, which I have examined, are short and semiacute, as contrasted with those of *freeborni* which are long, slender, and acute.

Dampf mentions the presence of nonpapillated hairs at the base of the claspers in the Mexican and American forms, but there is no indication of their extent or of a difference existing between the forms.

Vargas (1939a, p. 338) states, "Los pequeños pelitos que se encuentran cerca de la base nunca forman mancha como en *A. occidentalis, A. walkeri, A. atropos*, y que segun Root (1923), serviría para diferenciarlos de *A. quadrimaculatus*."

Dampf could find no differences in the form and makeup of the claspette lobes and their setae in specimens from California (*A. maculipennis freeborni*) and Mexico (*A. maculipennis aztecus*); and in a postscript-commenting on Hoffmann's paper (1935), he does not agree with that author that the spines of the claspette of the terminalia of *aztecus* differ by their form and aspect from those of the Cali-

fornia form. Hence, no distinctions between *aztecus* and *occidentalis* and *free-borni* on the basis of male terminalia can be made until further study of the three subspecies as we now know them has been undertaken.

Larva.—The most striking difference between the larvae of *A. maculipennis aztecus* and the American forms appears to be the position of the inner clypeal hairs (no. 3), which are separated sufficiently for another hair papilla to be placed between them Hoffmann, 1935; Vargas, 1939a). Hoffmann's photograph (p. 13) of the larval head of *aztecus* shows the characteristic *A. maculipennis* markings of the frontoclypeal sclerite, similar to *A. maculipennis freeborni*. The average number of branches of hair no. 2 of abdominal segment IV is three and of segment V is two (Vargas); Hoffmann says there are seven branches on IV; on the other hand, in *freeborni* both segments average two and in *A. maculipennis occidentalis* they are predominantly single. Hair no. 1 of segment II appears not to be a true palmate hair (Hoffmann). The palmate hairs (no. 1) on segments III to VII are approximately equal in size, the elements have straight margins ("con márgenes rectos") and terminate in a sharp point (Hoffmann, p. 16); Vargas (p. 337) states, however, "Pelos palmeados dorsales con una escotadura, cerca de la punta."

Egg.—Perhaps the most outstanding character of *A. maculipennis aztecus* is the egg. It is a flat egg with a rather narrow dorsal surface between the marginal frill. The poles or apices of the egg are more or less rounded, as compared with the rather pointed poles of *A. maculipennis occidentalis* and *A. maculipennis freeborni*.

Furthermore, the egg has a very dark appearance, almost black. Hoffmann (p. 17) says, "Los huevecillos son de color café claro sin manchas de ninguna clase. ... ya a primera vista por el color, que, no es gris." Dampf says (1936, p. 21) " ... en el *A. occidentalis* [*A. maculipennis aztecus*] de Méjico el color es siempre negro uniforme, correspondiente al carácter de la variedad *melanoon* Hackett." and later (p. 23) he says, "En el color corresponden los huevecillos méjicanos a los de California." With the latter statement, I cannot agree; the California eggs of both *A. maculipennis occidentalis* and *A. maculipennis freeborni* are gray.

The floats are large, occupying about 45 per cent of the total length (17–26 ribs). A great deal of uncertainty exists over the character of the float membrane. Hoffmann (p. 17) states "Las membranas intercostales llevan finísimas granulaciones." On the other hand, Dampf (p. 23) states, "En todos los huevecillos de *A. occidentalis* [*A. maculipennis aztecus*] que estudié no encontré ni una sola vez estrías transversales en los compartimentos. Como se vé en la Fig. 1, lámina VI, los primeros compartimentos tienen a veces ligera indicación de estrías transversales." Vargas (p. 336) does not discuss this point. I have examined eggs of *A. maculipennis aztecus* (kindly furnished by Vargas) and found that, compared with *A. maculipennis occidentalis* and *A. maculipennis freeborni,* the float membrane is rough; however, it is sporadically rough; not all areas of it are rugose to the same degree, and parts of the membrane may be smooth. See table 1 for a comparison of *A. maculipennis aztecus* with other American subspecies of *maculipennis*.

DISTRIBUTION
(Fig. 1)

A. maculipennis aztecus appears to be an inhabitant of the so-called "mesa central" of Mexico, a region lying above 5,000 feet and including altitudes of 7,400 feet or more. This subspecies is known from the following states: Puebla, Mexico, D. F., Michoacán, Guanajuato, Jalisco, Zacatecas, and Durango (Hoffmann, 1935; Dampf, 1936; Vargas, 1939a). Vargas, in confusing *aztecus* with the American inland form (since described as *A. maculipennis freeborni*), erroneously included in his distri-

bution of *aztecus* the states of California and New Mexico and in a subsequent paper (1939*b*) he includes *aztecus* in a key to the eggs of Californian anophelines. It should be pointed out at this time that following the period when *aztecus* was mistaken for *A. quadrimaculatus* and later *A. atropos*, the Mexican investigators have confused it with this inland form of American *A. maculipennis*.

From the Valley of Mexico, *A. maculipennis aztecus* seems to swing northward, hugging the eastern foothills of the Sierra Madre Occidental at least as far as Nombre de Dios and Constancia, Durango. It may occur in the mountains of central Chihuahua, but an extension beyond this point is doubtful. I have examined many specimens from southern California, Baja California, Arizona, and New Mexico and have found nothing but *A. maculipennis freeborni. Freeborni* undoubtedly occurs in Sonora and Chihuahua, but no thorough collecting has been done there.

COMPARISON OF OLD AND NEW WORLD ANOPHELES MACULIPENNIS

What is the relationship of the American *maculipennis* group to the *maculipennis* of Europe and Asia? At present, the Old World *maculipennis* group consists of ten or more forms which I believe can be segregated on the basis of morphological and biological affinities into the following six subspecies and their varieties: (1) *Anopheles maculipennis maculipennis;* var. *caucasicus* B. H. (?; described by Hackett and Barber, 1935, but given no name; see Stackelberg, 1937); (2) *A. maculipennis messeae;* (3) *A. maculipennis melanoon;* var. *subalpinus;* (4) *A. maculipennis labranchiae;* var. *sicaulti* (Roubaud), 1935; (5) *A. maculipennis atroparvus;* var. *fallax* (Roubaud), 1934; (6) *A. maculipennis cambournaci* (Roubaud and Treillard, 1936). *A. sacharovi* is here considered a distinct species, closely allied to *A. maculipennis.*

In contrast with this grouping, Bates (1940) has raised most of the forms of *maculipennis* to specific status, as follows: *A. maculipennis, A. messeae, A. melanoon melanoon, A. melanoon subalpinus, A. labranchiae labranchiae, A. labranchiae atroparvus,* and *A. occidentalis.*

The *A. maculipennis maculipennis* and *A. maculipennis messeae* subspecific groups of the Old World differ from the New World forms in the male, by having the external spine of the claspette normally blunt and rounded; the *A. maculipennis labranchiae* and *A. maculipennis atroparvus* subspecific groups tend to resemble our forms in this respect. This resemblance caused Dampf (1936) to consider these last two forms as subspecies of *A. occidentalis.*

Only one of our subspecies, *A. maculipennis occidentalis,* has the apex of the wing "silvery" or "bronze colored," whereas this is the usual color in the European forms. None of our subspecies have barred or spotted eggs. The inner clypeal hairs of the larvae are rarely minutely feathered at the tip, whereas these hairs are rather heavily branched in *A. maculipennis atroparvus, A. maculipennis messeae, A. maculipennis maculipennis, A. maculipennis labranchiae,* and *A. sacharovi* (letter from P. G. Shute, Ministry of Health, London); I have verified this in specimens of *sacharovi* collected in Macedonia by S. B. Freeborn. Certain differences are also manifested in prothoracic hair no. 9 (see p. 35), hair no. 1 of abdominal segment II and hair no. 2 of segments IV and V (see Hackett and Missiroli, 1935; Bates, 1939*b*). The external "spine" (hair no. 9) of the pupa in our forms is distinctly narrowly pointed, while it is blunt, at least in the English forms, probably *atroparvus* (Marshall, 1938). Other differences of a biological nature are manifested in the type of breeding place, overwintering habits, feeding preferences, swarming of males, and dispersal flights.

The closely related *A. lewisi* Ludlow (1920) has not been included in the synonymy of *A. maculipennis* for reasons explained in the following discussion.

A. lewisi was described by Ludlow from eight females and fourteen males, collected July 10–22, 1919, at Selenga and Verkhne Udinsk near Lake Baikal, Siberia. Ludlow states in her introduction that it belongs to the *maculipennis* group, yet certain differences are present, and since the Siberian mosquitoes are not well known, it seemed wise to describe it. Later, Edwards (1921) placed it in synonymy under *maculipennis* and it has appeared as such ever since. Christophers in his catalogue of the anophelini (1924), ventures that the type is in the Army Medical Museum, Washington, D.C. Ludlow mentions no types; hence she probably had before her a cotype series.

The U. S. National Museum now has in its possession 16 specimens (eight females, eight males) of *A. lewisi;* it has been possible for me, through the kindness of Alan Stone, to examine a male, including a terminalia preparation and female of the cotype series (Selanga, Siberia, July 10, 1919, through Miss Ludlow). The female is a large specimen, closely resembling a specimen of *A. maculipennis* from the Struma Valley, Macedonia, October 24, 1937 (R. C. Shannon). Its salient characteristics are as follows: wings 6 mm.; apical wing fringe somewhat pale, but mainly the result of reflection; wing maculations distinct but not smudgy as in *A. maculipennis occidentalis;* mesonotum bounded laterally by distinct dark bands; anterior border of mesonotum with small patch of yellowish white linear scales. The male terminalia preparation (U. S. National Museum, no. 1449, "Selanga, Siberia, July 10, 1919") exhibits the following characters: external lobe of claspette with one spine ("d" of Martini), which is *rounded* or *blunt;* internal lobe with spine "a" acute; hairs "v" and "s" also present; three pairs of leaflets on phallosome; group of nonpapillated hairs at base of dististyle; two parabasal spines; and lobes of ninth tergite long, slender, and pointed. It is evident from the form of spine "d" of the external claspette lobe, that *lewisi* belongs to the *A. maculipennis maculipennis*–*A. maculipennis messeae* subspecific groups. Furthermore, Beklemishev and Zhelochovtsev (1937) report *messeae* from Lake Baikal; in fact it is the only race of *A. maculipennis* recorded from western Asia, with the exception of *A. maculipennis atroparvus* which has been identified, on the basis of male terminalia, by Feng and Ch'in (1937), from North Manchuria. This evidence is highly suggestive that Falleroni's *messeae* (1926), originally described from Italy, is in reality Ludlow's *lewisi* (1920) and should be known as *A. maculipennis lewisi*. However, because the Siberian and Russian *messeae* may not be the same as either the northern or southern forms of the west-European *messeae,* it seems best to wait until additional evidence is forthcoming from the Lake Baikal region of western Siberia. *A. selengensis* was also described by Ludlow along with *lewisi,* based on two females collected at Selenga, Siberia, July 10, 1919, by First Lieutenant J. P. Kopecky. I have seen one of these females, both of which are in the U. S. National Museum, and can find no appreciable difference between it and *lewisi;* hence, *selengensis* remains in the synonymy of *A. maculipennis*. Since Ludlow failed to designate types, I hereby designate lectoholotype male, including the terminalia preparation (U. S. National Museum no. 77812) and lectoallotype female *A. lewisi* (U. S. National Museum no. 77813).

Thus *A. maculipennis occidentalis* the only American subspecies, which because of its geographical distribution into Alaska comes closest to the Old World forms, is quite distinct from *A. maculipennis messeae* (or *A. maculipennis lewisi*) as well as *A. maculipennis atroparvus,* provided the latter subspecies occurs in Western Asia.

The above evidence suggests that the New World forms are sufficiently different to be considered subspecifically distinct from *A. maculipennis;* furthermore, *A. maculipennis aztecus* appears to be the least closely related of the American forms. If this were true, our revised nomenclature would be: *Anopheles occidentalis occidentalis, A. occidentalis freeborni,* and *A. aztecus.* Future work may show that *occidentalis* and *freeborni* are specifically distinct; for the present, however, I prefer to consider the American *maculipennis* group as one part of a widely distributed Holarctic species, *Anopheles maculipennis* Meigen.

LARVAL BIONOMICS

BREEDING PLACES

Practically all of the observations that have been made on the larval biology of *A. maculipennis* in the United States deal with the subspecies *A. maculipennis freeborni.*

From the start of malaria investigations in California in 1910, Herms (1913) recognized that a difference existed in the preferential breeding places of *A. maculipennis (freeborni)* of the West and *A. quadrimaculatus* of the East; concerning the former he states: "A large proportion of the inland breeding places are traceable to faulty irrigation methods, particularly north of the Tehachapi." L. L. Williams, Jr. (1937, p. 22) gives this excellent description of the type of breeding place characteristic of *quadrimaculatus:* "It breeds almost wholly in still water that is relatively clean. It requires some sunshine, never being found in waters which are wholly unshaded, unless they have a type of flotage which casts narrow stripes of shade where the mosquito larvae may lie during a portion of the daylight hours. . . . Such flotage not only offers the requisite amount of shade, but an abundant food supply." *A. quadrimaculatus* has usually been termed a "pond breeder" since it rarely occurs in moving water.

On the other hand, *A. maculipennis freeborni* prefers clear, fresh, seepage water in pools sunlit for a part of the day. In the Sacramento Valley its larvae are commonly found in roadside depressions of overflow or seepage water (fig. 17) containing grass (frequently wire grass or spike rush, *Eleocharis palustris*) at least around the margins, and at times cattails (*Typha latifolia*). The flow of water in drainage ditches from rice fields is frequently slow enough to permit dense algal mats of *Hydrodictyon* and *Spirogyra* to form, in which larvae of *freeborni* and *pseudopunctipennis* find a suitable habitat.

In certain sections the rice fields themselves are suitable for the larvae of *A. maculipennis freeborni* and *A. pseudopunctipennis.* During the early stages of rice growth, mats of algae (*Hydrodictyon, Spirogyra,* and *Nostoc* in the Durham region) are formed, particularly around the margins of the fields and in the "dead" spots, which provide excellent harborage for the larvae. Although they are mainly found around the margins, they may also occur at considerable distances from the checks and are not necessarily associated with algae. This condition was observed in the Nelson and Richvale fields, in spite of the fact that these particular fields do not normally produce many anophelines, as demonstrated by Purdy (1925). There was very little water in the ditches; that in the fields apparently had stood for a long time and looked somewhat stagnant; it was about 14 inches deep. The blue-green algae, *Tolypothrix,* characteristic of these "hard-pan" rice fields were quite abundant. These observations were made on September 4, 1938, ten days before the water was to be drained from the fields.

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Fig. 17. A roadside seepage breeding place of *A. maculipennis freeborni*, characterized by a heavy growth of cattails. (Marysville, California)

Fig. 18 Around the margins of this borrow pit larvae of *A. maculipennis freeborni* may be found. (Marysville, California.)

Purdy investigated rice fields in the Butte County towns of Nelson, Durham, and Nord and in Anderson, Shasta County. Only the Nelson fields failed to produce anophelines, although there were breeding places in the seepages and drains; they were also the only fields in which the blue-green algae existed in abundance. During the summer (July 20, 1939), I made further observations of the rice fields between Biggs and Richvale; no anopheline larvae were found in the fields, which contained an abundance of *Tolypothrix*. The rice fields between Biggs and Nelson differ from others in the Sacramento Valley in that the soil in the former area is a "hard-pan"; consequently, not so much fresh water is required to retain the proper level. The water of the Nelson fields stands for long periods of time and becomes stagnant, *Tolypothrix* merely being an indicator of water fouling, whereas these other fields have a continual inflow of fresh, clear water which is ideal for the development of *A. maculipennis freeborni*. It should be pointed out here, that the greatest production of anophelines is not in the fields proper, but in the drains, seepages, and overflows around the fields.

Rice first appeared in California as a commercial crop in 1912 at Biggs, Butte County. In this state it is primarily grown in the Sacramento and San Joaquin valleys. The growing of rice requires the flooding of the entire acreage under cultivation from approximately June 1 to October 15. In these areas the summers are hot with low humidity. June, July, and August are the hottest months, with maximum temperatures ranging from 105° to 115° F.; during these periods there may be a daily range of temperature of 40° F. Although the winter months are usually mild, freezing temperatures may be encountered in December, January, and February. The Biggs Rice Field Station records an 18-year average annual rainfall of 20.07 inches. Considerable wind is encountered during the late fall and early spring months. For further information concerning rice culture in California as well as the related anopheline problem, the reader is referred to the paper by J. W. Jones, "How to Grow Rice in the Sacramento Valley" (1931), also to those by Freeborn (1916, 1917a, 1917b).

Although usually associated with sunny or semishaded places, *A. maculipennis freeborni* larvae may be found in deep shade. For instance, around the margins of the Nelson fields, they were found among a very dense growth of wire grass where very little sunshine could reach the water; in another place larvae were collected from spots so heavily overgrown with tall water grass (*Echinochloa crusgali*) that only the early morning sun could reach the water.

Shallow overflow areas, which continue to receive a certain amount of additional seepage and the like are frequently found to be supporting large larval populations of *A. maculipennis freeborni*. Occasionally they may be found in small semipermanent ponds, such as portrayed in figure 18, in the vicinity of Marysville, Yuba County (October 18, 1939); the plants associated with this pond among which the larvae were living consisted of bur marigold (*Bidens levis*), yellow water weed (*Jussiaea californica*), and cattails (*Typha latifolia*).

The pond type of breeding place would appear to be of more common occurrence as one proceeds northward, for Stage (1938a, p. 195) reports that "*Anopheles maculipennis* [*freeborni*] and *A. punctipennis*, and *Culex tarsalis* are found in almost every relatively clean, permanent pond, but it is a rare occurrence to take as many as three larvae per dip or to collect several adult anophelines in a 10-minute collection." I found a rather unusual type of pond breeding place of *A. maculipennis freeborni* in the Willamette Valley at Philomath, Benton County, Oregon (June 17, 1939). It was a small, deserted millpond about 30 feet in width; the surface was covered with a thick green scum, rarely associated with this species,

and entirely exposed to the sunlight; scattered plants of arrowhead (*Sagittaria latifolia*) occurred about the margins, and around their shaded bases anopheline larvae were encountered in considerable numbers, about five or six per dip. *Freeborni* larvae were also encountered in semishaded areas along the northeastern borders of Klamath Marsh in southern Oregon.

In eastern Oregon and Washington, where irrigation is practiced, Stage states that *A. maculipennis* (*freeborni*) breeds mainly in the border ditches, but also occurs in the so-called "marshes" which are wet with a few inches of water from mountain streams in the early part of the summer.

Rees (1939*a, b*) reports *A. maculipennis* (*freeborni*) in Utah breeding in small pools of irrigation water, around the margins of reservoirs and lakes, in ornamental pools and in puddles and "marshy" spots formed by springs and artesian wells.

The breeding places of *A. maculipennis* (*freeborni*) in the irrigated regions of New Mexico have been carefully studied by Barber and others (Barber, Komp, and King, 1929; Gerber, 1931; Barber and Forbrich, 1933; Barber, 1939). Barber distinguishes two main types of anopheline breeding waters in northern New Mexico, one type consisting of cool, clear water (shaded) and the other being wholly exposed to the sun and containing a dense accumulation of aquatic vegetation. The first habitat produces almost pure cultures of *A. maculipennis* (*freeborni*), whereas the latter is ideal for *A. pseudopunctipennis*. Of course, there are intermediate types, in which both anophelines grow side by side. Barber feels that daytime temperature is the determining factor. In the northern part of the state open pastures fed by irrigation water are the principal breeding places of *freeborni*. In southern New Mexico, *freeborni* favors well-shaded aquatic habitats. Drains, which are overgrown with reeds and other aquatic vegetation (*Myriophyllum*, etc.) and contain clear water, are the chief anopheline breeding places. In some, Barber traced a decreasing proportion of *freeborni* larvae from the shady margins outward. Needless to say, *pseudopunctipennis* was the predominant form in the exposed places. Springs and borrow pits are also important larval habitats.

A. maculipennis occidentalis occurs in a variety of aquatic habitats along the California coast. The observations I have made so far indicate a preference of *occidentalis* for impounded water habitats: permanent pools, lagoons, ponded creeks, and the like. In the immediate vicinity as well as just to the north of the city of Monterey, there are a number of large, cattail-bordered lagoons (fig. 19). On September 19, 1937, a visit was made to one of these lagoons just on the outskirts of the city; at the eastern end, large numbers of larvae of *occidentalis* and *A. pseudopunctipennis* in the first and fourth instars were found harbored among the fennel-leaved pondweed (*Potamogeton pectinatus*). A second visit was made on October 22; at this time the water level was lower, the pondweed had started to decline and was completely below the water's surface; however, around the margins of the lagoon, the grass had dried and drooped over into the water; among this vegetation the larvae of *occidentalis* were found. More recently *occidentalis* has been found breeding around the margins of San Felipe Lake, San Benito County; here the larvae occur in almost complete shade, living in a dense growth of cattails which are overhung by willows. I have collected *occidentalis* in a ponded creek at Valley Ford, Sonoma County, that had a rather heavy cover of duckweed (*Lemna minima*).

Other breeding places where one is likely to find *A. maculipennis occidentalis* along the California coast are the small seepages from hillsides, watering troughs, and the quiet, protected streams; in such places protection may be offered by algae (*Spirogyra, Chladophora, Microspora,* or *Vaucheria*), watercress (*Radicula* sp.),

or grass. Although I have not found *occidentalis* breeding in the beach pools formed by small creeks unable to empty directly into the ocean, it is known to occur just back of the beach. Undoubtedly it exists in such pools, for *A. punctipennis* is frequently encountered in this habitat. Quayle (1906) reports *A. maculipennis* (*occidentalis*) larvae as breeding in water that was distinctly brackish, in the wide tidal creeks of the San Rafael salt marshes, Marin County.

According to Hearle (1926), *A. maculipennis* (*occidentalis*) larvae in the Lower Fraser Valley, British Columbia, may be taken in "cottonwood flood-swamps, shallow pools under willow growth, and in permanent swamps and pools." In discussing a group made up of the following species, *Culex tarsalis* Coq., *Anopheles punctipennis* Say, *A. maculipennis* (*occidentalis*), *Culiseta inornata* (Will.), and *Culex*

Fig. 19. A breeding place of *A. maculipennis occidentalis*—impounded water at Monterey, California.

testaceous van der Wulp (*apicalis* Adams), he states that they have a preference for permanent and semipermanent bodies of water.

Dyar (1929) reports the presence of larvae "in the warmer algae-filled pools along the larger lakes and marshes" in Glacier National Park, Montana.

The observations of Owen (1937) in Minnesota bear out the above-mentioned larval preferences of *A. maculipennis occidentalis*. He found *A. maculipennis* (*occidentalis*) most frequently along the shores of semipermanent and permanent pools. They were also collected in temporary rain pools, woodland pools, marshes, open bogs, and along the borders of streams.

Our knowledge of the breeding places of *A. maculipennis aztecus* is based on what little information is available from Mexico through the papers of Hoffmann and Dampf. Hoffmann's (1935, 1936c) observations indicate *aztecus* favors canals, gutters, irrigation ditches, and pools of clear, standing water containing algae and an abundance of protozoa; also favored are lakes, such as Pátzcuaro (Michoacán) which support dense masses of water lilies, tules, and pondweed. Apparently the Mexico *A. pseudopunctipennis* is much more exacting in its requirements with respect to the purity of the water than is *aztecus;* as a consequence, in the vicinity of Mexico City, where the purity of the water has suffered somewhat as a result of urbanization, *pseudopunctipennis* has gradually disappeared and *aztecus* has in-

creased in numbers. This appears to be in sharp contrast to conditions existing in California, where Freeborn (1926) states that *pseudopunctipennis* continues to breed for some time in pools after they have become too foul for *A. maculipennis (freeborni)*. The observations of Dampf (1936) sustain those of Hoffmann; he stresses accumulations of fresh, clean water containing much aquatic vegetation and exposed to the sun. One place, in particular, was mentioned which seems to bear out Hoffmann's statement concerning the toleration of *aztecus* larvae of water fouling; Dampf regularly found larvae at Peñón Viejo or Peñón del Marqués, D. F., in a small ditch which drained water from a swimming pool and which was exposed to the sun only during the early part of the day.

ALTITUDINAL DISTRIBUTION

A. maculipennis freeborni larvae occur over a wide vertical range, being found from sea level along the southern California coast or near sea level in the delta region of the Sacramento and San Joaquin rivers up to at least 5,480 feet at Sierraville, Sierra County (Herms, 1929). It is doubtful if *freeborni* will be found much above this altitude in the Sierra, otherwise it probably would have been encountered before now; I have on several occasions attempted to locate *freeborni* larvae in the higher mountains without success. The only anopheline taken above this elevation in California is *A. pseudopunctipennis;* it was found at 7,300 feet. East of the Sierra *freeborni* is known from the Owens Valley towns of Lone Pine, Independence, and Bishop, ranging from 3,728 to 4,450 feet in elevation (Aitken, 1939a). In New Mexico Barber and Forbrich (1933) report *A. maculipennis (freeborni)* at elevations of 5,600 feet in the region of Española, Rio Arriba County and farther south in Doña Ana County (Las Cruces) at 3,800 feet. According to Rees (1934), *maculipennis (freeborni)* has not been taken above 7,500 feet in Utah.

In California *A. maculipennis occidentalis* is found at sea level and in the lower elevations of the Coast Ranges. I am unfamiliar with the altitudinal distribution in the north except for the fact that *occidentalis* is found, for instance, in the river valleys of the Fraser in British Columbia, the Mayo in the Yukon, and the Mackenzie in the Northwest Territories; Dyar records it from the North Fork Ranger Station, Glacier National Park, which is about 3,200 feet elevation.

A. maculipennis aztecus is restricted to the high central plateau of Mexico, at elevations of 5,000 feet or more.

ADULT BIONOMICS

SEXUAL ACTIVITIES

Hackett (1937b, p. 47) says, *"Anopheles maculipennis* when mating observes in general the ritual of the swarming of the males which occurs out of doors over some fixed object such as a hay stack or gable, beginning as Shannon happily records, just as Venus begins to shine in the west." The swarming of males of *A. maculipennis freeborni* is a common sight during the summer evenings in the Sacramento Valley. I have observed swarms at Davis, Yolo County, at about 7 o'clock in the evening; no particular preference appeared to be manifested by the males in the sites chosen; some swarms hovered near trees or shrubs, but others danced out in the open fields away from any objects. While on a collecting trip east of the Sierra, I observed swarming of *freeborni* at Coleville, Mono County, May 25, 1939. It was about 7 o'clock in the evening and the light was getting dim; the swarm was dancing to leeward of a patch of wild roses; occasionally, a slight breeze sprang up and the swarm would suddenly disappear, only to reappear as soon as the wind ceased.

Although females were biting me at the time, none were observed to dart into the swarm and effect copulation.

To my knowledge Freeborn's (1923) is the only record of swarming of *A. maculipennis occidentalis*. Two swarms were observed October 8, at Leverett Pond, Massachusetts, one of which was dancing over a small pine tree and the other was in an open space near the pond 75 yards from the first. This is an interesting example of overlapping of the range of two anophelines, for one of these swarms was composed of males of *A. quadrimaculatus*, the other being a swarm of *A. maculipennis* (*occidentalis*).

No mention of swarming of *A. maculpennis aztecus* is made by either Hoffmann (1935) or Dampf (1936), but both authors state that *aztecus* is readily reared in the laboratory, copulation being effected in receptacles as small as a lamp chimney. Hoffmann met with success using cages about $16 \times 12 \times 12$ inches; during the winter oviposition was obtained by keeping the temperature at 64.4°–68° F.

Attempts have been made at various times to establish laboratory colonies of *A. maculipennis freeborni* without much success. On one occasion workers in this laboratory succeeded in carrying *freeborni* through five generations, and at another time two generations were obtained, but in both attempts the resulting populations were weak and finally died out. On both occasions the work was done during the late fall. I have also obtained unsatisfactory results. Adults, brought into the laboratory, have laid eggs which have been cultured and the progeny reared through to adults, but no matings have ensued. Containers or cages of various sizes, from bobinet-covered wine glasses to a glass case seven and a half feet high and four feet square, have been used at room temperature; wine glasses and cages, $8 \times 8 \times 9$ inches, covered with bobinet, have been placed in an incubator at 74° F. and 84 per cent relative humidity without results. Furthermore, these attempts to stimulate matings have occurred at various times of the year. At the time of this writing, a small colony of *freeborni* (or *freeborni* hybrids) is under observation, the progeny of a female (A–613) collected at Stanford University, November 29, 1939. They are housed in a bobinet-covered cage, $20 \times 20 \times 20$ inches, at room temperature; a thick layer of cellulose cotton lying on the top of the cage, which is kept constantly wet, along with a large bowl of water within the cage, keeps the relative humidity at about 74 per cent. A piece of black canvas has been placed over the cage to reduce the light intensity during the day. Only on two occasions have the males been observed to swarm; both times were in the evening (about 6:30), when a desk lamp was held sufficiently near the cage to permit vision. Copulation was not observed at any time, nor have subsequent dissections of females disclosed the presence of sperm in the spermatheca. Although the ovaries have developed to complete maturity on a number of occasions, following repeated blood meals, the females have always died before oviposition took place; one female carried mature eggs with her for a period of over two weeks, yet finally died without their being deposited; she was removed from the room temperature cage to an 86° F. incubator for five days with the hope of stimulating oviposition, but without success. It is my opinion that *freeborni* is a eurygamic form primarily, and will only mate with difficulty in captivity.

A small colony of *A. maculipennis occidentalis*, the progeny of a female (A–615) collected at Stanford University, November 29, 1939, is also under observation in a similar cage. As yet no swarming or mating has been observed in these individuals; occasional females have been dissected from time to time, but none have been found inseminated. These individuals may be in a state of "semi-hibernation" since the females accept blood meals, but the sexual impulses have not as yet been stimu-

lated. I am rather inclined to think, in spite of the negative laboratory evidence, that *occidentalis* along the California coast exhibits stenogamy, because the frequent strong winds blowing off the ocean may have a prohibitive action on the swarming phenomenon.

EGG-LAYING HABITS

The maximum number of eggs deposited by one *A. maculipennis freeborni* female in this laboratory is 315 (199 plus 186, two layings) with an average 209 per female (Herms, and Freeborn, 1920); these observations were made during the months of May, June, and July at Vina, Tehama County, and comprise 30 layings. A subsequent paper by Herms and Frost (1932) reports the following oviposition records made during the 1931 season in Sutter Basin, Sutter County; the maximum for one female was 288, average 195. A misprint should be pointed out in that paper; in recording the previous results of Herms and Freeborn, the maximum for one female was given as 385 instead of 315. Hansen (1939) included certain additional figures in her discussion of *freeborni* from Sutter Basin; 14 ovipositions during February gave a maximum of 160, with an average of 129 eggs per female; 10 ovipositions during May gave a maximum of 309, with an average of 206 eggs per female. My records, gathered during January, February, March, April, August, and December at Sunol, Alameda County, and in the Sacramento and San Joaquin valleys, are as a whole somewhat smaller than those given above; 25 ovipositions have been observed, with a maximum of 268 and an average of 106 eggs per batch. The combined averages of all records to date suggest that in the laboratory *freeborni* lays about 170 eggs at a time.

I obtained several batches of eggs of *A. maculipennis occidentalis* during March, July, and August at Point Reyes Station, Marin County, Valley Ford, Sonoma County, and Castroville, Monterey County; the maximum for one female was 149, average 95.

All females which I brought into the laboratory in order to obtain eggs were fed on my arm. The feeding time was approximately three minutes; this may be contrasted with the rapid feeding time of *Aëdes dorsalis* (Meigen), our common salt marsh or fresh-water pest mosquito, which is about 50 seconds.

Herms and Freeborn (1920) describe completely their observation, one of the first, of the method of oviposition of *A. punctipennis*. Egg deposition commenced at 9:45 P.M. and lasted for 19 minutes, 174 eggs being deposited. I was fortunate enough to be able to witness the act of oviposition in *A. maculipennis occidentalis*, from Point Reyes Station, Marin County, on March 20, 1939. The first egg appeared at about 5:40 P.M., and the procedure lasted for ten minutes; at the end of this period 128 eggs had been deposited. No mention was made by the above authors of the part played by the wings in oviposition, the eggs merely being freed by the twitch of the abdomen. In *occidentalis* I noticed that the first jerk of the abdomen extruded the egg in a vertical position; the second jerk brushed the egg off against the wing, using the latter as a backboard, and another egg appeared in view. Except for this slight variation, both anophelines acted very similarly.

INTERBREEDING ACTIVITIES

W. L. McAtee (1920), in a paper dealing with the specific, subspecific, and varietal categories of insects, refers to investigators in ornithology and mammalogy who freely use the term subspecies; a subspecies, he states (p. 47), "is a geographic race, a part of a species marked by average differences in characters which intergrade with those of subspecies occupying different, though usually adjacent parts

of the general range of the species, along the common boundary of which intergradation is complete."

It was mentioned previously that certain areas are known where interbreeding between *A. maculipennis occidentalis* and *A. maculipennis freeborni* probably may be taking place, such as in the vicinity of Stanford University, parts of British Columbia, and Montana. At least we know that overlapping occurs. Both *occidentalis* and *freeborni* occur together in the region from San Luis Obispo south to Ventura, which is the present known southern range of the former. Both subspecies have been taken together under the same bridge at Stanford University. On November 29, 1939, a female (A–613) was collected there which resembled *occidentalis* in the large wing maculations and very melanic appearance—but unfortunately the wing apex was denuded. This female deposited a batch of *occidentalis*-like eggs, but the resulting adults were typical *freeborni*. This observation, although not conclusive, suggests that interbreeding does occur along the common boundary of these two forms.

SEASONAL INCIDENCE

The seasonal incidence of *A. maculipennis* (*freeborni*) in the interior valleys of California has been thoroughly discusssed by Freeborn (1932) who, basing his study on a correlation of adult and larval populations, found that in the central Sacramento Valley there are six generations a year (fig. 20). In mid-February there is an initial dispersal flight of overwintering females, which lay their eggs and die. Following this there is a period of nine to ten weeks when the mosquito population is in the water. The first spring brood occurs in early May, at which time males make their appearance, and is followed by a gradual decrease in adults until late June, when there is a striking drop which is not regained until September 1. The greatest population is reached in late September and early October, after which there is a dwindling in numbers until mid-January, the last males having disappeared in November. As pointed out by Freeborn (1932, p. 218), "The mid-summer depression of adults is not reflected in the larval collection but is replaced by a peak during the last week in June, which represents a well-defined generation."

During the latter part of October and early November there is a second dispersal flight of the so-called "prehibernation" forms. They invade areas previously free of mosquitoes and are very finicky and nervous in biting activities, rarely engorging. The "hibernating" forms are active throughout the winter, coming out and biting promiscuously on warm days and in heated buildings; at no time during this period do the ovaries mature, in spite of occasional blood meals, and the fat body is well developed. Rarely, I have obtained egg batches in the laboratory from such overwintering forms. The larvae have disappeared by late December and do not reappear until mid-February at the close of the spring flight.

The adult population slump during July and August has been called the period of "aestivation," and as Freeborn demonstrates (1932, p. 215), "is the result of unfavorable weather conditions, and is brought about when the maximum daily temperature is in excess of 90° F. and the daily evaporation from a white ball atmometer is in excess of 70 cc." (fig. 21).

I carried on observation on *A. maculipennis freeborni* through the fall and winter of 1938–1939 in the Coast Ranges at Sunol, Alameda County. Complete collections, 65 in all, usually twice a week, were made between August 2 and April 17, under a concrete bridge across Calaveras Creek (fig. 33). The graph (fig. 22), based on monthly totals, demonstrates the trend in the population of *freeborni,* males and females, through the fall and winter months. *A. punctipennis* and *A. pseudopunctipennis* also occurred at Sunol, and their populations may be correlated in figure 23.
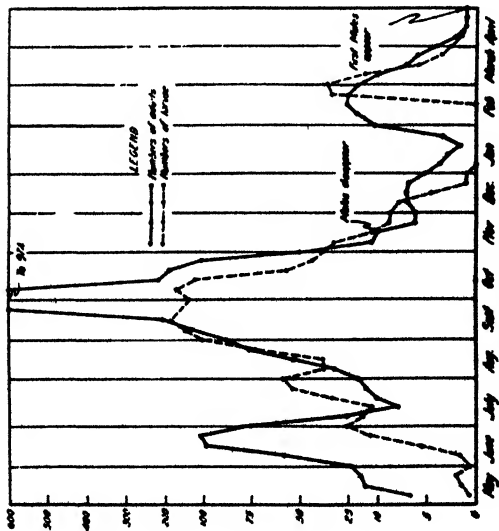
Fig. 20. Seasonal abundance of adults and larvae of *A. maculipennis freeborni* in the Sacramento Valley, California, represented by weekly catches (from Freeborn, 1932).
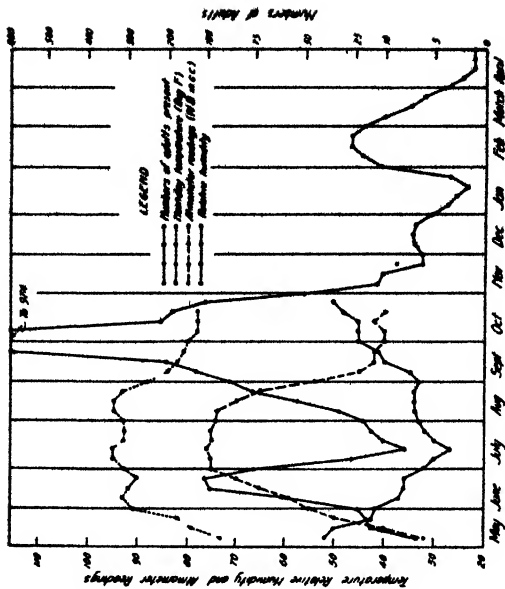
Fig. 21. Weekly catches of adults of *A. maculipennis freeborni* in the Sacramento Valley, California, with the noonday temperatures, relative humidity, and the weekly average of 24-hour records of the white ball atmometer (from Freeborn, 1932).

The greatest numbers of *freeborni* occurred in August, following which there was a gradual decline in individuals; after the low in January, their numbers increased again in February and March, probably as a result of warmer weather and greater activity, in this respect corresponding fairly well with what Freeborn found in the Sacramento Valley. Too much significance probably should not be attached to
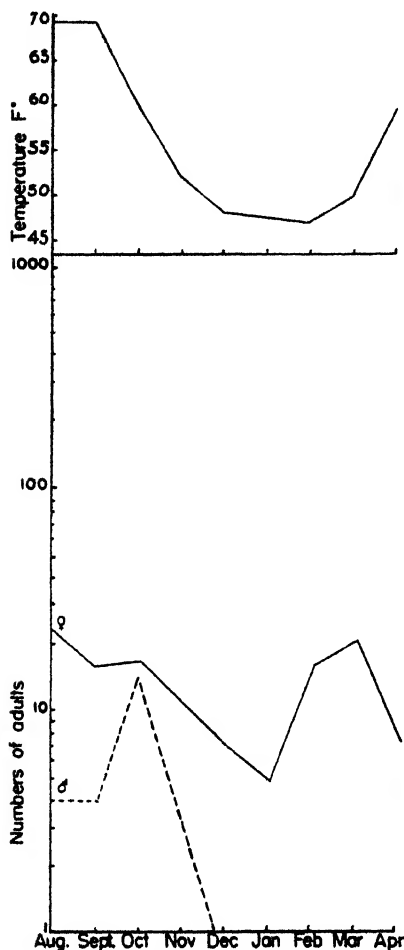
Fig. 22. The incidence of adults of *A. maculipennis freeborni* during the fall, winter, and spring of 1938–1939 at Sunol, California.
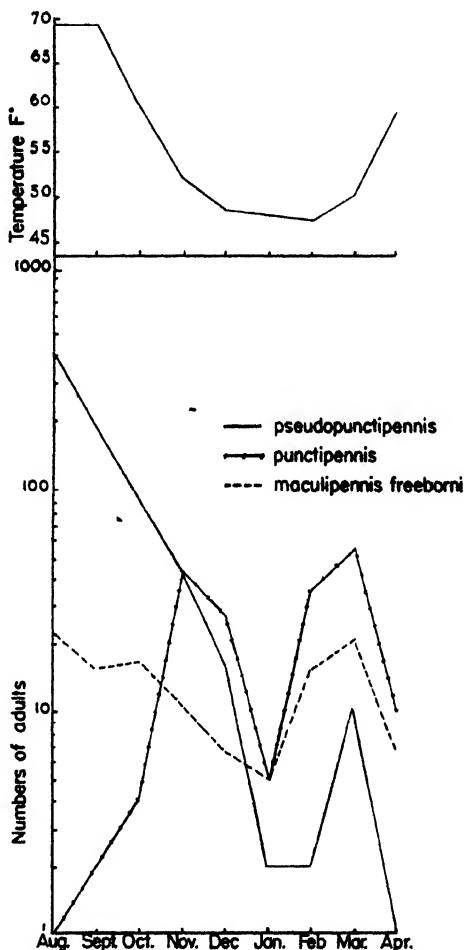
Fig. 23. The incidence of females of *A. pseudopunctipennis, A. punctipennis* and *A. m. freeborni* during the fall, winter, and spring of 1938–1939 at Sunol, California.

the marked rise in the male population in October; no males were found after the first week in November.

Unfortunately, an atmometer was unavailable for this study; a sling psychrometer was used at the time of the collections which was usually about 10 A.M., but inasmuch as these were sometimes of necessity made at odd hours, the readings were not always uniform. Therefore, monthly temperatures and precipitation, recorded by the U.S. Department of Agriculture Weather Bureau for the near-by town of Livermore, are appended (table 4).

At the outset of this study an attempt was made to correlate the larvae with the adults; however, this was found to be unsatisfactory since the larval population in the nearby breeding areas was practically a pure culture of *A. pseudopunctipennis*, and the pools soon became unsuitable for making quantitative dips.

Certain evidence gathered suggests that breeding may be going on at a very slow rate during the winter months in the Coast Ranges, but not in the central valleys. For instance, a female was collected on January 3 with ovaries in stage two (Christophers, 1911) of development; on January 17 a few fourth instar larvae, very sluggish, were collected near Sunol; in the laboratory they emerged February

TABLE 4

MONTHLY TEMPERATURE AND PRECIPITATION FOR LIVERMORE,
CALIFORNIA, 1938–1939

Month	Temperature	Precipitation
	Degrees Centigrade	*Inches*
August, 1938............................	20.67	0 00
September.............................	20.67	Trace
October...............................	15.00	1 00
November.........................	10 89	1.08
December.............................	9.11	0 52
January, 1939.........................	8.61	2 40
February.............................	8 44	1 57
March	10.11	2.18
April.................................	15.11	0.53

1. One female was collected on January 20 in stage three of ovarian development, and again on February 17, and 21, females were found with mature ovaries. From this time on, females captured were usually replete with eggs.

Observations have been carried on by Greiner (1936) on the overwintering habits of *A. maculipennis (freeborni)* in Bernalillo and Valencia counties, New Mexico. He found that it went into true hibernation in that area but made no mention of a fall dispersal flight or feeding during warm winter days. Adult females without blood and immature ovaries, but with well-developed fat bodies, were found in barns during December and January; the last males were captured on October 31 and no larvae were found later than November 29. During the latter part of February and in early March the overwintering females again became active, fed, deposited their eggs and died.

I have not yet gathered any significant data on the overwintering of *A. maculipennis occidentalis* in California; it is quite probable that breeding may go on at a slow rate during the winter months. At no time of the year have large populations been observed. Owen's (1937) observations on the hibernation of *maculipennis (occidentalis)* in Minnesota, suggest that this is undergone in the adult stage in those regions; no larvae were collected after August 13, although they undoubtedly occur at a later date, or before May 30. A peak is reached in late July, following which the pools dry up. He also found extreme cold fatal to overwintering adults. Dyar (1929) reports that hibernating adults entered a cabin on the west side of Glacier National Park in the early spring. No dispersal flights of *A. maculipennis occidentalis* have as yet been observed.

Hoffmann (1935) states that *A. maculipennis aztecus* may be found at all times of the year in the Valley of Mexico, but it appears to show a preference for the dry

season. Females are found in inhabited houses throughout the winter. The males are scarce or disappear completely during the coldest weeks, but a new brood appears with the advent of warmer weather. The larvae are found throughout the year, even during periods when ice may have formed on the water. No dispersal flights have been reported by either Hoffmann or Dampf (1936); the latter also points out that the winter climate of the Valley of Mexico is considerably warmer than that of the Sacramento Valley; the minimum temperature during November, December, and January for the Sacramento Valley (five years) was 2.9° C. and for the Valley of Mexico (fifty years) 6.67° C., while the average for the hottest days during the same period was 18.7° C. in the Sacramento Valley and 23.0° C. in the Valley of Mexico.

DISEASE RELATIONSHIP

A. maculipennis freeborni is the most important vector of malaria in western America. Although no laboratory experiments have been undertaken to prove its susceptibility to the various species of *Plasmodium,* enough epidemiological evidence has been gathered to prove *freeborni* to be the most dangerous anopheline of the West; this was recognized as early as 1913 (Herms).

It is definitely a house-invading mosquito and readily attacks man. During the summer of 1920 at Vina, Tehama County, California, Herms (1921c) made daily collections from May 12 to July 13. Of 77 anophelines found indoors, 50 were *A. maculipennis (freeborni)* and 27 were *A. punctipennis;* in the outdoor series of 343 anophelines, 102 were *maculipennis (freeborni)* and 241 were *punctipennis.*

Similar observations have been made in New Mexico, as reported by Barber and Forbrich (1933). In Doña Ana County 52.2 per cent of 226 mosquitoes collected inside were *A. maculipennis (freeborni)*, the others were *A. pseudopunctipennis;* on the other hand, a collection of 1,412 mosquitoes outdoors yielded only 4.2 per cent *maculipennis (freeborni)*. Moreover, they found that many more *maculipennis (freeborni)* collected indoors were blood engorged than were *pseudopunctipennis.* Dissections were made at Española, in the northern part of the state, and in Doña Ana County, in the southern part. Of 868 *maculipennis (freeborni)* examined, 1.4 per cent were positive both for salivary glands and stomachs, whereas of 263 *pseudopunctipennis* examined none was positive.

At the present time malaria is probably endemic in only three of the western states: New Mexico, in the valleys of the San Juan and Rio Grande rivers; California, in the San Joaquin and Sacramento valleys; Oregon, in the Willamette Valley.

Table 5 shows the incidence of malaria in California from 1906 to date as prepared by Miss I. M. Stevens, Supervising Morbidity Statistician, California State Department of Health.

The first antimalaria campaign in the United States was started by W. B. Herms, February 12, 1910, at Penryn, Placer County, California, and was quickly followed by campaigns in Oroville, Bakersfield, and Los Molinos. There are now 22 mosquito-abatement districts and two pest-abatement districts carrying on active control work in the state. The decrease in malaria in California can be in large part attributed to the work of these organizations as well as to the crusading of Herms (1919b).

Morbidity figures reached a low in California in 1932, 0.8 per 100,000 population; since that time there has been a gradual increase reaching a high in 1938, 358 cases or 5.4 per 100,000. Table 6 shows the morbidity figures for the ten counties, all in the central valleys, having the highest malaria incidence since 1932. It is of interest to note that much of this malaria has been associated with the migratory labor camps. All three species of *Plasmodium* occur in California; *P. malariae* is rare and *P. falciparum* is relatively uncommon.

Stage and Gjullin (1935) state: "Malaria was first reported in the Oregon Territory in 1829 and 1830 and was the contributing cause of much sickness and death among the Indians and early settlers along the Columbia River at that time. Malaria

TABLE 5

MALARIA IN CALIFORNIA

(per 100,000 population)

Year	Cases	Case rate[b]	Deaths	Death rate[b]
1906	....	....	111	5.9
1907	....	....	70	3.5
1908	....	....	80	3 6
1909	....	....	112	4 9
1910	....	....	113	4.7
1911	....	....	121	4.8
1912	....	....	101	3 9
1913[a]	77	2 8	77	2 8
1914	342	12 1	70	2 5
1915	527	17.9	45	1 5
1916	935	30.7	54	1 8
1917	749	23.7	47	1.5
1918	667	20 4	55	1 7
1919	1055	31 3	28	0 8
1920	484	13 7	34	0 96
1921	269	7.2	43	1 14
1922	215	5.4	31	0.78
1923	196	4.7	32	0 76
1924	107	2.4	24	0 54
1925	77	1 7	29	0 63
1926	94	1.9	9	0 19
1927	58	1.1	15	0 30
1928	77	1 5	17	0 32
1929	100	1.8	16	0 29
1930	94	1.6	12	0 21
1931	80	1.3	7	0 12
1932	51	0.8	5	0.08
1933	84	1 3	3	0 05
1934	184	3 0	5	0 07
1935	173	2.8	6	0 08
1936	189	3.0	6	0 09
1937	171	2.6	9	0 14
1938	358	5.4	8	0.12
1939	296	4.3	0	0.00
1940	175	2.5	6	0 09
1941	139	2.0	5	0 07

[a] Previous morbidity records not kept.
[b] Estimates based on 1930 and 1940 census figures.

has remained endemic to a greater or lesser extent in the Willamette Valley for more than 100 years." Malaria first became a reportable disease in Oregon in 1918, since which time the morbidity figures shown in table 7 have been accumulated (see Stage and Gjullin).

I sent a questionnaire to the health officers of the various western states, from some of whom information was obtained relative to the incidence of malaria.

TABLE 6
COUNTIES HAVING HIGHEST MALARIA RATES, 1933–1939

Counties	1933	1934	1935	1936	1937	1938	1939	Total
San Joaquin	..	68	64	25	13	20	8	198
Yolo	..	..	4	1	1	66	65	137
Yuba	1	3	6	24	29	16	34	113
Tulare	1	5	3	3	4	76	14	106
Sutter	..	1	8	28	6	5	9	57
Butte	9	7	1	4	1	24	4	50
Sacramento	4	5	4	4	6	1	15	39
Fresno	4	2	2	..	.	17	11	33
Kern	1	11	1	4	8	4	3	32
Kings	..	..	..	1	4	16	2	23
Total	17	102	93	94	72	245	165	788
Total for state	84	184	173	189	171	358	284	1,443

TABLE 7
MALARIA IN OREGON

Year	Cases	Year	Cases	Year	Cases
1920	9	1925	1	1930	34
1921	4	1926	25	1931	20
1922	2	1927	16	1932	53
1923	1	1928	9	1933	26
1924	4	1929	16	1934	23

TABLE 8
MALARIA IN WASHINGTON

Year	Cases	Location
1915	2	Yakima County
1923	1	Chelan County
1928	2	Yakima County (1)
		Kittitas County (1)
1929	3	Yakima County (2)
		Pierce County (1)
1930	3	Yakima County
1932	1	Seattle
1933	1	Spokane County
1934	3	Yakima (1)
		Pacific (1)
		Seattle (1)
1935	1	Seattle
1936	1	Olympia
1938	4	Jefferson (1)
		Kitsap (1)
		Yakima County (2)
1939	1	Seattle

It appears that Washington has had no indigenous cases of malaria, at least in recent years; however, until the last five years, epidemiological investigations have not been complete enough to determine in all cases the source of infection. The majority of cases have occurred among the migratory labor population coming into the Yakima Valley during the hop and fruit harvest. The morbidity figures for the state of Washington as shown in table 8 were obtained from R. H. Fletcher, M.D., Acting State Director of Health.

TABLE 9

MALARIA IN COLORADO

Year	Cases	County	Deaths	County
1930	..	....	2	Baça (1) Logan (1)
1931	4	Mesa (1).. .... Weld (3).	..	
1932	5	Adams (1)........... .... Boulder (1)........ .... El Paso (1)..................... Logan (1)...... .... Pueblo (1)........		
1933	3	?...............................	1	Mesa
1934	4	?...............................	..	
1935	2	?...	..	
1936	..	....		
1937	1	Morgan		
1938	6	Mesa (3)... .... Otero (1)..................... Rio Grande (1)....... .... Weld (1).. ....,....	1	San Miguel
1939	9	Custer (1)........... .... Denver (2). . ... Jefferson (1).. .... Lake (1) .... Pueblo (3)......... .... Weld (1)......·.................	.	

E. L. Berry, Director, Division of Public Health, informs me: "There is essentially no malaria in Idaho. A few years ago there were a few cases, I think not to exceed two or three, reported from the locality near Horse Shoe Bend, Boise County ... These are the only indigenous cases I know anything about."

B. K. Kilbourne, M.D., Epidemiologist, records no indigenous cases of malaria in Montana.

During the period 1929–1939 there have been two deaths attributed to malaria in Nevada. An Indian child died at the Nixon Reservation, Washoe County, in 1932, but the case received no laboratory diagnosis. The other case was a male, who died at Boulder Dam in 1933, having contracted the disease in Alabama. This information was furnished by J. J. Sullivan, Jr., Vital Statistician, Nevada State Department of Health.

There have been five cases in recent years recorded from Wyoming, two in 1932, one in 1934, and two in 1936; it is believed by N. H. Savage, M.D., Director, Division of Epidemiology, that all cases were imported.

During the period 1930–1939 Colorado reports 38 cases and four deaths, without saying which, if any, of these cases were contracted within the state. Of the 16 affected counties only Mesa and San Miguel counties lie west of the Divide, in the domain of *A. maculipennis freeborni;* Mesa County is known to contain this mosquito. It would not be surprising if *freeborni* were found in Rio Grande, another of the affected counties, which is east of the Divide, since it is known from the Rio Grande Valley farther south, at Española, New Mexico. Table 9 gives the list of reported cases and deaths attributed to malaria in Colorado during the past ten years, as supplied by J. S. Cullyford, M.D., Director, Division of Epidemiology.

I have been informed by L. G. Donnelly, Assistant State Director of Malaria Control, that dependable malaria morbidity and mortality figures for New Mexico do not exist. Malaria is known to be present in the irrigation regions of the Rio

TABLE 10

MALARIA IN DOÑA ANA COUNTY, NEW MEXICO[a]

Year	Local new infections	Recurrences	Total	Year	Local new infections	Recurrences	Total
1923	0	2	2	1928	719	216	935
1924	0	3	3	1929	302	176	478
1925	3	4	7	1930	212	166	378
1926	7	20	27	1931 (to Dec)	68	46	114
1927	319	1	320				

[a] From Barber and Forbrich (1933), and comprising cases reported to the County Health Office. They explain that the County Health Officer "classifies the infections of the years 1925 to 1929, inclusive, as follows: (a) malaria contracted previous to coming to Doña Ana County, 43.01 per cent; (b) cases contracted in Doña Ana County, 56.84 per cent."

Grande and San Juan river valleys. Barber and Forbrich (1933, p. 611) list the cases for Doña Ana County during the years 1923–1931 (see table 10).

No information has been received from the state health departments of Arizona, Utah, and Oregon.

A. maculipennis occidentalis probably plays little or no part in the transmission of malaria, perhaps because it occurs in a cool climate or because of the nature of the mosquito itself—its biting habits and susceptibility to plasmodial invasion. Probably both factors are important.

The sexual phase of the *Plasmodium* requires for its completion a temperature of 61° F. (16° C.) or above. The summer isotherm of 60° F. cuts off the greater part of the California coast from about San Luis Obispo northward; this cooler coastal belt is the region inhabited by *occidentalis.* Moreover, no malaria has been known from the California coast. The same is true of the Oregon coast.

Malaria may occur elsewhere in the range of *A. maculipennis occidentalis,* for Riley (1930) reports this disease in Minnesota and Wisconsin. Several species of anophelines occur in this region, including *A. quadrimaculatus,* but the part of *occidentalis* in transmission is not known.

A. maculipennis aztecus and *A. pseudopunctipennis* are considered by Hoffmann (1931) to be the transmitting agents of tertian malaria in the Valley of Mexico (see *A. quadrimaculatus*). On the other hand, Vargas (1939a), who reports on a case of "anophelism without malaria" in the state of Mexico, states (p. 336) "en Méjico aparentemente no desempeña papel de tanta importancia."

SUMMARY OF SPECIES COMPLEX

The American *maculipennis* group is considered for the present to comprise the following:

Anopheles maculipennis occidentalis (Dyar and Knab) 1906.
Anopheles maculipennis freeborni Aitken, 1939.
Anopheles maculipennis azteous Hoffmann, 1935.

Anopheles maculipennis occidentalis is the "silver-" or "bronze-tipped" melanic form of the cool western seacoasts and northern regions. Its preferential breeding places are primarily shaded areas of ponds, lagoons, and other forms of permanent water. *Occidentalis* is of little or no importance as a disease disseminator.

Anopheles maculipennis freeborni is the brown, unicolorous form of the warm, irrigated western regions, west of the Divide. Fresh seepage water and roadside pools are the preferred larval habitats. Although the evidence is largely epidemiological, *freeborni* is considered to be the West's most important vector of malaria.

Anopheles maculipennis aztecus is the large, long-winged, linear-scaled subspecies of the Mexican plateau. *Aztecus* larvae favor canals or irrigation ditches of fresh water containing algae and other vegetation. The status of this mosquito as a malaria vector in Mexico is disputed.

Anopheles pseudopunctipennis Theobald

Anopheles pseudopunctipennis Theobald, 1901, 2:305.
Anopheles peruvianus Tamayo and Garcia, 1907.[12]
Proterorhynchus argentinus Brethes, 1912, 1:15.
Anopheles tucumanus Lahille, 1912, 23:253.
  var. *boydi* Vargas, 1939*b*, 19:356.

Type locality.—"Grenada, February (Dr. Hatton, per Dr. Daniels)."
Description: female.[13]—HEAD clothed with upright, triangular scales on occiput, those on vertex white, with black ones laterally, ocular bristles black, those between eyes white; palpi as long as proboscis, with white rings in middle of segment III (long segment) and at base and apex of segment IV, almost entirely black on V; proboscis black. THORAX, mesonotum with pale, median, pruinose gray stripe bounded laterally by dark bands, vestiture of narrow straw-colored scales, a tuft of white ones just posterior to head; wing scales black and white or pale yellow, the pale scales forming long spot on costa, occasionally spreading to apex of subcosta and R_1 (1st vein), another pale spot at apex of costa, tip of R_1 and preapex of R_{2+3} (2d vein, upper branch), Sc with basal pale spot involving R_1 and one at middle involving R_1 and origin of R_{2+3}, stem of R_{2+3} dark except small pale patch at cross vein, R_{4+5} (3d vein) with small pale patch at base, a long one in middle, somewhat variable in length, and patch at tip, media (4th vein) dark-scaled except pale patch at base, one at cross veins and apices of branches, cubitus (5th vein) pale-scaled to fork except for subbasal black spot, Cu_1 dark except for basal, middle, and apical pale patches, Cu_2 with dark patch subapically, anal vein (6th) pale basally and dark apically, wing fringe dark except at ends of veins; tips of femora and tibiae narrowly pale-scaled. ABDOMEN brownish black with numerous brownish hairs.

DISCUSSION

No description of the egg, larval, and pupal stages, or of the male terminalia of *A. pseudopunctipennis* have been made from the type locality. Since this mosquito is widely distributed over two continents and certain regional variations appear to exist, I feel that for the present a formal description of these two stages cannot be given; however, the following account attempts to point out the variations and differences existing among the North American forms and those found in Mexico, Central and South America.

Terminalia.—The anatomical makeup of the male terminalia has been particularly confusing. The description appearing in Howard, Dyar and Knab (1917, p. 1021), states: "Unci [phallosome] slender, columnar, short, rounded at tip." Likewise, both Dyar (1922, see under *Proterorhynchus* Brethes, p. 102) and Root (1923) mention that the phallosome is without leaflets. All of these observations had been made on material from California and Texas. Shortly thereafter, Root (1924*b*) examined specimens from Tampico, Mexico, and discovered the presence of two pairs of delicate leaflets, the apical pair being toothed on both sides and the other on one side only. Root states that these leaflets, because of transparency and their tendency to stick to the apposed surface of the anal lobe (proctiger), have probably been overlooked previously, but he suggests that they may not exist in the northern form, *"franciscanus,"* described by I. McCracken in 1904 from Stanford University. The fact that Root (1922, p. 383) had noted a difference in the hair (no. 11) of the antennal shaft of larvae from Central America and California, strengthened his suspicions concerning this variation. In the description of *A. pseudopunctipennis* in "The Mosquitoes of California," Freeborn (1926) states that there are no leaflets on the phallosome; furthermore, the subsequent observations of Frost (1932), based on material from the Sutter Basin, Sutter County, confirmed this description. However, both Dyar (1928) and Matheson

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[12] *Anopheles multimaculatus* Gastiaburú (from Peru) is seen in the literature occasionally, but it appears to be a thesis name only.
[13] Description based on specimens from Stanford University, California.

(1929), in their comprehensive treatises of the American mosquito fauna, agree with Root. More recently, Komp (1937) has examined male material from Argentina, Panama, Costa Rica, Mexico, the island of Grenada, the states of Texas and New Mexico, and a single specimen from California (Stockton, San Joaquin County), and in all he found leaflets to be present. In South America, apparently, the existence of an ornamented phallosome is unquestioned (Shannon and Del Ponte, 1927).

I have attempted to find the reason for the discrepancies existing in the literature. Collections have been made throughout the entire range of the species in California. Stained terminalia mounts of specimens from widely scattered areas were prepared and carefully examined; material was also obtained for study from Arizona (T. K. Ryan), New Mexico (M. A. Barber), Mexico (W. C. Earle), and from South and Central America (A. Stone, F. Campos R., and W. H. W. Komp). Although this study is still incomplete, the results of these examinations indicate that the form adorned with the leaflets is of wide occurrence in California, specimens having been collected in the following places: San Diego County (Bonsall, Doheny Park, Escondido, Jacumba, and San Ysidro), Riverside County (Elsinore), Kern County (Bakersfield, Canebrake Creek on Walker Pass), San Luis Obispo County (San Luis Obispo), Tulare County (Farmersville), Monterey County (Carmel and Little Sur rivers), Santa Cruz County (Watsonville), Mariposa County (Bagby), Tuolumne County (Lyons Dam), Alameda County (Sunol), Yolo County (Madison), Sutter County (Robbins), Glenn County (Orland), Mendocino County (Willits), and Del Norte County (Wonderland Park). At the same time there is considerable material possessing the unornamented phallosome, thus confirming the observations of Freeborn and Frost; this form has been found in the following counties: San Diego, Riverside, Kern, San Luis Obispo, Monterey, Mariposa, Alameda, Sonoma, Yolo, Sutter, Placer, and Mendocino. In most specimens the proctiger and ninth tergite and sternite were dissected away from the phallosome, yet no leaflets are visible. It is quite possible that in mounting the specimens the leaflets adhere to the body of the phallosome or are brushed off, yet it does not seem probable that several specimens from the same locality would act similarly. The occasional experience of finding both types of terminalia present in mosquitoes from the same locality is somewhat disconcerting, but this occurrence may have a possible explanation, as will be subsequently shown.

It is significant to note that the leaflets, when appearing in the California forms, are usually extremely delicate and sometimes very hard to discern; this was also true of specimens from San Fernando Mission, Baja California, approximately one third of the distance down the peninsula. On the other hand, extremely well-developed and distinctly serrated leaflets were observed in males from Arizona (Wilcox), New Mexico (Leasburg and Carlsbad), Tennessee (Memphis), Oaxaca (Rincón Antonio), Baja California (Morelos and San José del Cabo), Costa Rica (Puerto Viejo and San Antonio), Colombia (Barranquilla), Ecuador (Guayaquil), Peru (Colonia Perené, in Chanchamayo), and Bolivia (Cuevo, Entre Ríos, and Camargo).

The leaflets of the Arizona specimens were extremely bushy, suggesting the presence of three or four pairs, whereas the California forms appeared to have no more than two pairs of leaflets; if the latter were serrate, this was extremely hard to discern. Barber (1939) found the leaflets of New Mexico forms varying from one to four pairs, the latter being most common; Barber also states (p. 353), "Leaflets were usually serrate, but often very slender without distinguishable teeth. There was much variation in their form and size; tiny rudimentary leaflets were not

uncommon." Barber's observations suggest that in New Mexico and Texas there may be two forms of *pseudopunctipennis,* one resembling one of the California forms with the delicate leaflets and the other resembling the Mexico forms with well-developed leaflets. Vargas (1939*b*) found the leaflets in Mexico specimens varying from one to four pairs, and Dampf (1939) one to five pairs.

Through the kindness of G. F. Ferris, I had the opportunity of examining the paratype series of *A. franciscanus* (five males and one female, Stanford University, California, May 5, 1903, lot 456, sub. 1), a species which was synonymized with *A. pseudopunctipennis* by Howard, Dyar, and Knab (1917). Since no description of the male terminalia was given by McCracken (1904), I was anxious to know the appearance of the phallosome; the delicate leaflets, typical of other California specimens of *pseudopunctipennis,* were present. Hence, we can associate the California forms having the ornamented phallosome with *franciscanus.* Apparently no type was designated by McCracken, so I take this opportunity to designate the lectoholotype male, including terminalia preparation, and the lectoallotype female of *A. franciscanus,* both of which are at Stanford University.

In all slide mounts of terminalia yet examined the appendages of the dorsal (outer) lobe of the claspette are not three stout, sharp-pointed setae as one reads in all the descriptions, but are three very broad, flat spines, actually leaflike in shape, with rounded, bent tips; in this respect they approximate the shape existing in *A. barberi* (Coquillett). Occasionally the inner appendage of the series takes on the form of a narrow, sharp-pointed spine or a blunt-pointed spine; a smaller straight spine may or may not be present at the base of this claspette lobe. I called this matter to the attention of S. B. Freeborn, who kindly verified the findings. Similar findings have been encountered by both Vargas (1939*b*) and Dampf (1939) in Mexico. Dampf points out the close similarity of the terminalia of *A. pseudopunctipennis* and *A. hectoris* Giaquinto Mira, the former usually having two internal claspette spines as compared with three in *hectoris;* the "leaflets" of the external claspette of *hectoris* are larger and more pointed, and its three serrated leaflets of the phallosome are larger, more strongly chitinized, and the middle one is the largest.

Variations in the number of parabasal spines are not uncommon in certain regions, as pointed out by Root (1934), who found that they may range from one spine on a side to three and four on a side. As yet, I have seen nothing but the normal two-paired condition in California specimens.

Wings.—In the discussion of *A. pseudopunctipennis,* Howard, Dyar, and Knab (1917, p. 1023) state, "*Anopheles franciscanus* differs slightly, the fourth vein media being dark scaled, ... whereas it is whitish before the fork in typical *pseudopunctipennis....* This form (*franciscanus*) is the usual one in the northern part of the range of the species, but it is gradually evanescent in more southern localities. We have seen many specimens which are intermediate in this respect and have integradient specimens from the same rearings in Panama. We are satisfied that the difference, so far as it exists, is not of specific value, but only a slight variation."

Vargas (1939*b*) has made similar observations in Mexico; he states (p. 357), "En mucho cientos de ejemplares observados en Temixco, Mor., se notaron exactemente las mismas variaciones del color de las escamas, en hembras que uniformemente depositaron el mismo tipo de huevo."

An examination has been made of the *A. pseudopunctipennis* material in the University of California collection, and in a random sample of 363 specimens, taken from all parts of the state, not one was found with the fourth vein (media) predominantly pale-scaled before the fork (fig. 24). A similar color pattern existed

in specimens from Arizona, New Mexico, and Baja California (Santo Tomás, San Fernando Mission, and Punta Prieta. Those from San José del Cabo differed, however, as in the case of the terminalia, in having the fourth vein predominantly pale-scaled before the fork. Specimens from Oaxaca (Rincón Antonio), the Valley of Mexico, Colombia (Barranquilla), and Venezuela (Maracay) were pale-scaled; four specimens from Costa Rica (Puerto Viejo) were intermediate, but in the southern part of the range of *pseudopunctipennis*, Ecuador (Guayaquil), Peru (Colonia Perené, in Chanchamayo, and Bolivia (Cuevo, Entre Rios, and Camargo), the dark-scaled color pattern of the fourth vein reappeared.

An additional difference in the wings of *A. pseudopunctipennis* from the United States and those from regions farther south has been noted. The wing of *pseudopunctipennis* from Venezuela (fig. 25), as figured by Cova-Garcia (1939, pl. IX),
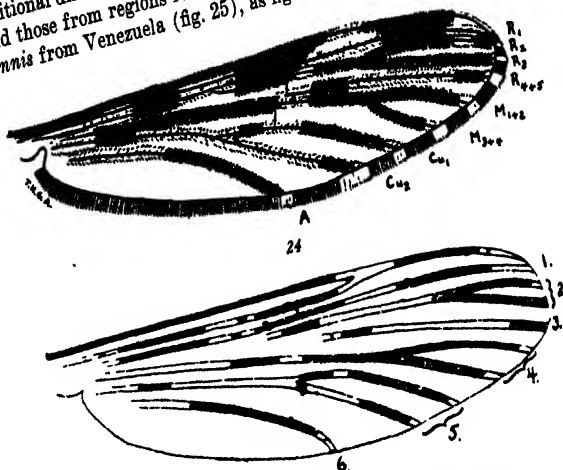
Fig. 24. Wing of California *A. pseudopunctipennis*.
Fig. 25. Wing of Venezuela *A. pseudopunctipennis* (from Cova-Garcia, 1939).

shows the stem of the second vein (R_{2+3}) as being white-scaled except for a sub-basal black patch; also the upper branch of the second vein is white apically. I found this color pattern present in specimens from Colombia (Barranquilla), Costa Rica (Puerto Viejo), and Mexico (Rincón Antonio and San José del Cabo). The second vein in California specimens, however, is entirely dark-scaled, except for a subapical white patch on the upper fork and a tiny patch on the stem near the cross vein. In the material from Baja California (except from the Cape region), Arizona, New Mexico, Ecuador, Peru, and Bolivia the scale color of the second vein, like that of the fourth vein (media), resembles that found in the California forms.

Although Howard et al. (1917) report variation in the wing maculations of the Panama *A. pseudopunctipennis*, and Vargas (1939b) reports likewise for specimens from Temixco, Morelos, there appears to be a marked distinction between the forms from the United States and the greater part of Baja California and the forms from Mexico, Central America, and northern South America, while the type occurring in the more southern areas of the range of the species tends to resemble the northern forms. Undoubtedly, the black-winged form in which the second and

fourth veins are largely dark, extends southward into Mexico and intermingles with the more common "pale-winged" *pseudopunctipennis* of that region. Hoffmann (1931, p. 524) states, "In the littoral zone of the Pacific, *A. pseudopunctipennis* extends along the entire coast from Guatemala to California. Its subspecies, *franciscanus* McCracken, inhabits only the northern part, extending as far south as into the northern districts of the state of Sinaloa." Presumably, Hoffmann recognizes *franciscanus* on the basis of wing markings. In the light of Varga's (1939*b*) observations, this range might be increased as far as the state of Morelos.

Palpi.—Of notable interest is the fact that western species of *A. pseudopunctipennis* have the apical segment of the female palpi almost entirely black-scaled. This coloration appears to prevail as far east as west Texas. However, material from Brownsville, Texas, resembles that from Mexico and more southern regions in having white-tipped palpi.

Larvae.—The larvae of *A. pseudopunctipennis* are readily recognized by the clypeal hairs (anterior and posterior, nos. 2, 3, 4), which are single; also, the elements of the palmate hairs are drawn out into long, narrow, slender points. Komp (1937) points out a character on the postspiracular plates, namely two tails which are produced upward at right angles to the plane of the plates. He states, "As a means of positive identification of the species, this character seems superior to any of those hitherto used because of its size and easy visibility. In fact the tails may be seen with a 20 × lens." This character has apparently been overlooked by most investigators, but as pointed out by Komp, it had already been described by Shannon and Del Ponte (1927) in the Argentina *pseudopunctipennis*. Komp examined material from Argentina, Panama, Mexico, Costa Rica, and California and found the tails present on larvae from all of these regions.

In a recent description of the larval chaetotaxy of *A. pseudopunctipennis* from Temixco, Morelos, Vargas (1940) reports the presence of this character in Mexico forms. As a result of these observations I became interested in knowing whether the "tailed" larvae occurred in California. A great many larvae have been examined from various parts of the state, and in spite of Komp's statement to the contrary, no "tailed" forms have been found, either in fresh or preserved material; rarely, specimens have been encountered where a slight indication of tail is noticeable, but nothing comparable with the long appendages figured by Komp. A few specimens from New Mexico, received from M. A. Barber, and from Arizona have been examined and very short tails are visible. Specimens more recently examined from Texas (Brownsville) distinctly exhibit the "tailed" condition; moreover, this character is utilized by King, Bradley, and McNeel (1939). Two larvae from Comondú, Baja California, about two-thirds the distance down the peninsula, have well-developed "tails" on the postspiracular plates. Through the kindness of W. H. W. Komp, larvae were received from Argentina and Bolivia. Both lots exhibited tails, those from Bolivia being the better developed of the two. Furthermore, Komp has informed me by letter that the Bolivia forms have smaller tails than the forms from Panama. Cova-Garcia's description (1939, table 4) indicates that the larvae of *pseudopunctipennis* from Venezuela are devoid of "tails."

Further differences between the *A. pseudopunctipennis* larvae from California and regions farther south are to be found in the antepalmate hairs (no. 2) of abdominal segments IV and V. Present observations indicate that hair no. 2 in California specimens varies in having from one to three branches, average 1.8, on segment IV, and is single on segment V. In 30 specimens, one exhibited three and another two branches on segment V. On the contrary, larvae from Arizona, New Mexico, Mexico (Vargas), Bolivia, and Argentina have single antepalmate hairs on both segments.

Vargas (1940) mentions that hair no. 2 on segments IV and V may occasionally be bifurcated at the base as well as minutely at the tip.

The antennal hair (no. 11) may be branched or single in California larvae, both forms being almost equally common. This hair appears to be single in specimens from Arizona, New Mexico, Mexico (Vargas), and Bolivia; specimens which I examined from Argentina had the single hair, but Shannon and Del Ponte (1927, p. 37) figure this in the branched form. This figure, furthermore, shows the lateral abdominal hair (no. 6) of segment IV as being pinnately branched, but in the specimens examined (Río Grande, Jujuy, June 19, 1936, S. Mazza) they appeared no different from *A. pseudopunctipennis* larvae from other regions. Cova-Garcia (1939) also states that these hairs of segments IV and V are pinnately branched in Venezuela specimens.

It seems, therefore, that the California *A. pseudopunctipennis* again differs from those of more southern regions, namely in certain larval characters such as the antennal hair (no. 11), antepalmate hairs (no. 2) of abdominal segments IV and V and the structure of the postspiracular plate.

Pupae (fig. 26).—The pupae of *A. pseudopunctipennis* can be readily distinguished from other western American anophelines by the lateral spine (no. 6) of segment VIII, which is unbranched; this spine is pinnately branched in *A. maculipennis occidentalis*, *A. m. freeborni*, and *A. punctipennis*. Moreover, hairs B and C in *pseudopunctipennis* are much stronger than those of *maculipennis* and *punctipennis*.

Unfortunately, I have no pupae of this species from Mexico or South America to compare with California forms. Senevet (1934) described the pupa of *A. pseudopunctipennis*, presumably from South America, but as yet I have not seen this paper. Specimens of *pseudopunctipennis* from Arizona (Yuma), Imperial County, California (Holtville), and Alameda County, California (Sunol), have been examined, see figure 26. The lateral spine is particularly well developed on segments IV to VIII, those on segments VI and VII being the longest (½ length of segment). Hair B on segments IV to VII is usually single with two weakly developed subsidiary branches. Hair C on segments IV to VII is usually single, rarely with one or two weakly developed subsidiary branches. The specimens from Yuma and Holtville were observed to have a heavy, wavy line across the base of the paddles. Moreover, the serrations on the outer lower border of the paddles are extremely well developed. Average length of paddle, 1.00μ, average width, 0.540μ, ratio 1.8:1.
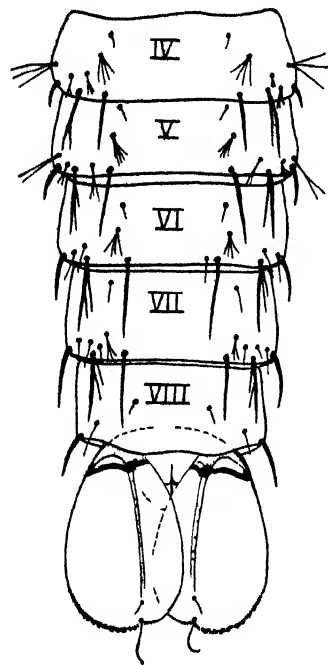
Fig. 26. Pupal chaetotaxy of *A. pseudopunctipennis* (see fig. 3 for terminology).

Eggs.—The oviposition records for *A. pseudopunctipennis* in California are the lowest for the three anopheline species occurring in this state. The figures given by Herms and Freeborn (1920) are, maximum for one female 157, average per female 106; and those given by Herms and Frost (1932) are, maximum 210, average 151. The greatest number obtained by the writer was 283, with an average of 140 per female (113 ovipositions). Vargas (1939b), working in Morelos, Mexico, obtained a maximum of 292 eggs, average 139.

The eggs of this species, as originally described by Herms and Freeborn (1920) from a single batch of eggs obtained at Vina, Tehama County, June 4, 1920, ranged from 512μ to 528μ in length. They differ from most anopheline eggs in that the

27   28
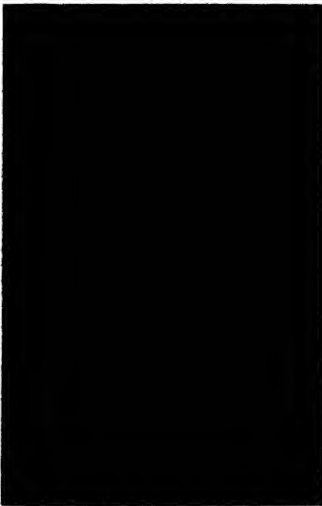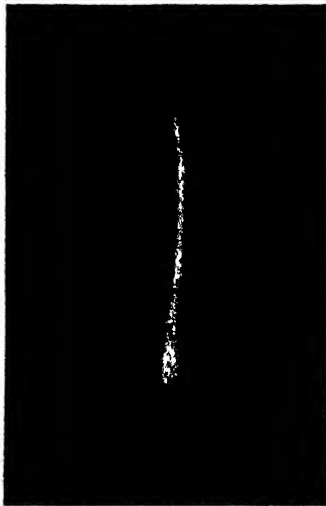
29   30

Fig. 27. Egg of *A. pseudopunctipennis franciscanus,*
dorsal view.
Fig. 28. Same, lateral view.
Fig. 29. Egg of the variety *boydi,* dorsal view.
Fig. 30. Same, lateral view.

floats are "represented by a fusiform closely appressed area, approximately 270μ long lying on the dorsal side of the egg and nearer the blunt end." (Figs. 27, 28.) A median line divides the two floats, each of which is composed of twelve compartments. The exochorion, having polygonal reticulation, flares out to form a

translucent, striated "collar" completely encircling the narrow, posterior end, except for a triangular, median incision. This egg hangs below the surface of the water, usually vertically but sometimes at an angle, supported by surface tension on the frill-like "collar."

During a subsequent study of anopheline eggs by Herms and Frost (1932) this type of egg was not discovered. Instead a new egg was described, in which the floats completely encircle the periphery (figs. 29, 30) and are composed of from 45 to 47 chambers. Its length, exclusive of the floats, ranged from 493μ to 510μ, inclusive of floats, from 510μ to 544μ; the floats varied from 15μ to 25μ in width. At no time was the frill-like collar of the original egg evident. Occasionally, however, the floats are closely appressed to the surface of the egg in such a manner as to somewhat resemble the original description. The chorion within the floats is finely granular and that of the ventral surface (exochorion) has a delicate polygonal reticulation. This egg lies flat on the surface of the water with the floats usually extended.

Rozeboom (1937a) described the egg of *A. pseudopunctipennis* (fig. 31) from the Canal Zone (Pedro Miguel); this egg compares favorably with Herms and Freeborn's description. It differs, however, in that the floats are larger, the mean float length being 376μ, and there is a greater number of chambers, the extremes ranging from 22 to 38 ridges, average 29.6; the floats meet at the midline and are fused together; the eggs vary in length from 480μ to 575μ with an average of 520μ.

The original type of egg remained "lost" until I obtained it in two egg batches laid by females collected at Eureka, Humboldt County, July 21, 1937. Since then I have found this type of egg batch in the following localities: Jacumba, San Diego County (August 3, 1937); Oxnard, Ventura County (August 4, 1937); Cayucos (August 9, 1937) and Estero (July 31, 1940), San Luis Obispo County; Carmel and Little Sur rivers (July 7, 1938) and Bradley (July 31, 1940), Monterey County; Stanford University, Santa Clara County (December 8, 1939, topotype of *franciscanus*); Aetna Springs (July 28, 1940), Napa County; Lanes Redwood Flat, Mendocino County (July 24, 1937); and Sunol, Alameda County. During the course of investigations at Sunol I obtained: 23 ovipositions of this type of egg, provisionally termed "atypical" because of its rather rare occurrence in this state, during the months of March, April, May, August, September, October, November, and December; 45 ovipositions of the "typical" form (of Herms and Frost) during July, August, September, October, November, and December; and in the same months 13 ovipositions of a type I term "transition" (fig. 32) to describe eggs intermediate between the typical and atypical forms.

All three types of eggs have been obtained from Sunol. Both main types are known to occur at Eureka, Lanes Redwood Flat, Aetna Springs, and the Little Sur River and one batch of transition forms has been obtained at Stanford University. Within each batch of typical and atypical eggs, one finds that all of the eggs are of the same type. Within a batch of transition eggs one finds eggs ranging from typical, in which the floats completely encircle the periphery, through forms in which the floats have come together at the narrow posterior end and are pinching off the collarlike frill, to the atypical, in which the float is completely separated from the posterior frill. In the atypical eggs there are frequently forms which have an extensive float area, somewhat approximating that existing in the Panama eggs, although the float chambers proper would appear to be larger and the floats may meet at the midline. But they are not fused together. Occasionally one finds atypical forms in which there may be a small buttonlike area of exochorion which apparently has pinched off from the end of the float proper (fig. 32 C, D). One batch of atypical eggs (A–452) was particularly interesting in that the floats had been
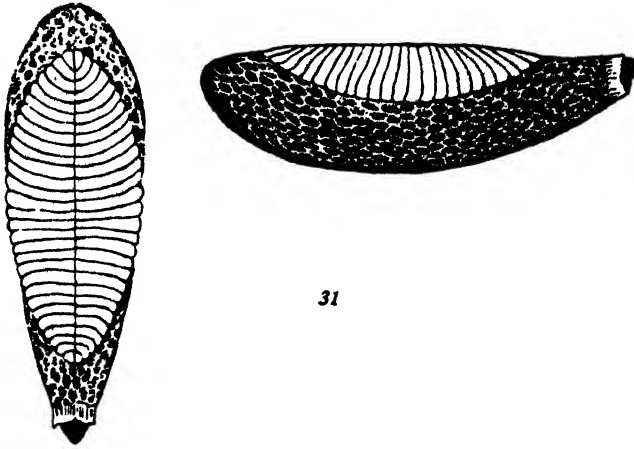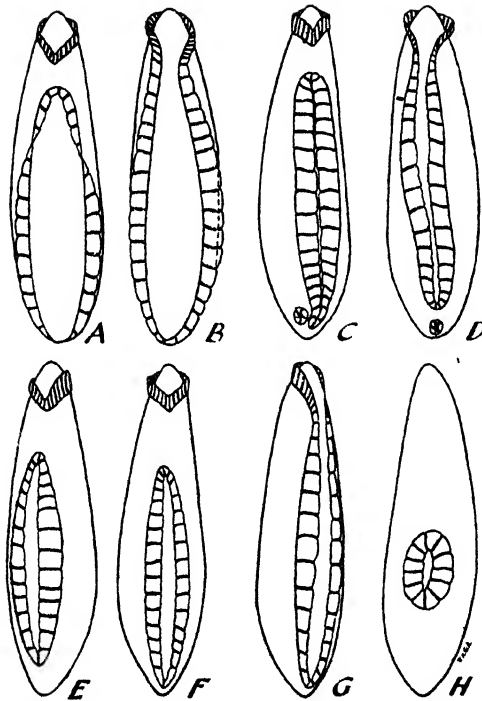
Fig. 31. Egg of Panama *A. pseudopunctipennis*
(from Rozeboom, 1937).
Fig. 32. Transition eggs of *A. pseudopunctipennis* from Sunol,
California. *H* is an unusual form of *A. p. franciscanus.*

reduced to a small circular area in the middle of the egg and were composed of about 12 chambers; furthermore, the collarlike frill at the apex of the egg was completely lacking (fig. 32 H).

The maximum number of typical eggs (Herms and Frost) obtained by me from one female was 227, with an average of 138; for the transition eggs, the maximum

was 237, average 150; and for the atypical eggs (Herms and Freeborn), the maximum was 283, average 126.

Egg measurements have been made of the Sunol eggs as follows:

Atypical eggs: length, 452.5μ–517μ (average 480.13μ); width, 125μ–142.5μ (135.38μ); float length, 256.25μ–352μ (304.69μ); float width, 62.5μ–80μ (75.19μ); float chamber width, 31.25μ–40μ (37.59μ); float chambers on a side, 14–20 (17, or 16 ridges or ribs). These figures differ somewhat from those given by Herms and Freeborn, but undoubtedly considerable variation exists, particularly in such an area as Sunol, where both types and intermediate eggs are found.

Transition eggs: length, 450μ–506.25μ (average 486.12μ); width, 131.25μ–143.75μ (138.04μ); floats, 61.25μ–93.75μ (75.51μ); float chamber width, fairly constant at 37.5μ. Typical egg: measurements were found to compare favorably with those given by Herms and Frost (1932).

The average measurements of the Sunol atypical eggs are shown in table 11,

TABLE 11

Comparison of Similar *A. pseudopunctipennis* Egg Types

Region	Length	Width	Float length	Float width	Float chambers
California (Aitken)	420 13μ	135μ	304 69μ	75 19μ	17
California (Herms and Freeborn)	512–528		270 00		12
Panama (Rozeboom)	520 00	158	376 00	158 00	30
Mexico (Vargas)	523 00	140	381 00	140 00	31

where they can be compared with the same egg type described by Herms and Freeborn (1920) from Vina, California, Rozeboom (1937) from Panama, and Vargas (1939b) from Morelos, Mexico. The eggs from Mexico and Panama are larger and have more float chambers than those from California.

Barber (1939) briefly describes the eggs of *A. pseudopunctipennis* from New Mexico and Texas (Del Rio), indicating that they resemble the "collared" type as described by Herms and Freeborn. I received a vial of these eggs from M. A. Barber, and although dried and rather frayed, they appear to resemble more closely those from Mexico and Panama in the number of floats; this point should be checked carefully. Through the kindness of W. C. Earle, eggs were obtained from Morelos, Mexico (May, 1938); these, as shown above in the work of Vargas, compare more favorably with those from Panama than with the California type.

Vargas (1939b) has described a new species from California, *A. boydi,* which is based on the *A. pseudopunctipennis* egg type described by Herms and Frost and heretofore referred to in this paper as "typical"; the species can only be recognized in the egg stage. Vargas states (p. 361), "Ahora bien, con una especie tan bien caracterizada como el *A. pseudopunctipennis* se ha confundido durante largo tiempo un *Anopheles* típicamente norteamericano, de distribución limitada que tiene por centro el Estado California, especie sin importancia en la transmisión del paludismo, que propongo llamar *A. boydi* y que se distingue con facilidad del *A. pseudopunctipennis* por los caracteres de los huevos, siendo los adultos facilmente confundibles entre sí." He mentions no type specimens or type locality, except California.

Since all three types of eggs may be found in California in the same locality, interbreeding between the two forms may be taking place, as will be pointed out

later. I am inclined to believe, that *A. boydi* cannot be considered specifically distinct from *A. pseudopunctipennis*, but may be, however, a good variety. Vargas failed to avail himself of the name *franciscanus* when describing his new species, in spite of the fact that it was available, presumably because the eggs as well as the terminalia of *franciscanus* were unknown. Fortunately, however, as a result of collecting in the type locality of *franciscanus*, I have been able to obtain eggs which theoretically can be associated with the anopheline described by McCracken; they are the so-called atypical type of Herms and Freeborn and hence the association of the name *boydi* with the typical eggs of Herms and Frost is not altered.

Matheson and Hurlbut (1937) and Hurlbut (1938*a*) have demonstrated that *A. walkeri* oviposits in the eastern United States a winter type of egg and a summer type of egg, each being morphologically distinct. Two forms are oviposited by *A. pseudopunctipennis* in California; however, both forms are to be found at all times of the year; furthermore, I have been able to obtain hatching at any time. Lawlor (1940) has described a second type of *A. pseudopunctipennis* egg, and considers the typical egg and his newly described type, which he calls "unusual," as merely "seasonal" eggs. The new egg variant appears in January and February. Gibbins (1933), in Africa (Fort Portal, Uganda, 5,100 feet), has found extreme variation existing in the eggs of *A. marshalli* Theobald, the various forms being found within the same egg hatch; his observations were based on the eggs of three females. Rozeboom (1938) has demonstrated the same sort of transition series in eggs of *A. strodei* Root from Panama as occurs in the California *pseudopunctipennis*; it appears from Rozeboom's paper that these eggs were collected from water in the natural breeding place of *strodei*, hence one might assume that they were probably not all from the same female. He makes no attempt to explain the variation, merely emphasizes that the races of anophelines are best not designated until sufficient study has been made of their physiology and habits.

DISTRIBUTION

Because of its extensive north and south distribution, its inconsistencies as a vector of malaria in the Americas, and because of the conflicting reports concerning its morphology and habits, *A. pseudopunctipennis* has come to be an extremely interesting mosquito to study. As L. L. Williams, Jr., recently wrote (1937, p. 23), "Why should *pseudopunctipennis* spread malaria in Mexico and Argentina and not in the Pecos Valley of New Mexico and western Texas, where the density of *pseudopunctipennis* is high? The answer awaits the entomologist." The most extensive treatises covering the habits, distribution, and disease relationship of this species are the excellent papers by Shannon, Davis, and Del Ponte (1927), Shannon and Davis (1927), and Hoffmann (1931, 1937).

Roughly the range of this species includes the western regions of the North and South American continents lying between the parallels of 42° north and 32° south. At present the species is known as far north as Wonderland Park, Del Norte County and Yreka, Siskiyou County, California.

Two records (Corvallis, Benton County, Oregon, September 6; Forest Grove, Washington County, November 17–December 7, Cole), have been reported from Oregon (Cole and Lovett, 1921), but Freeborn (1926) was doubtful of these because the specimens were lost and the northernmost known occurrence of the species, at that time Sonoma and Tehama counties, California, did not coincide with any barrier except that of latitude. The fact that it has been found breeding in northwestern California suggests that it might occur at least in southern Oregon. Stage and Gjullin (1935) do not list it among the anophelines present in that state.

In California *A. pseudopunctipennis* is widely scattered; the only areas free of it are parts of the northeastern counties and southeastern desert regions that do not have sufficient water. It is fairly abundant throughout the Sacramento and San Joaquin valleys, is very common in the adjacent foothills, and reaches its greatest development in southern California, south of the Tehachapi Mountains and along the coast.

From the Imperial Valley (east of Holtville, May 13, 1939, Aitken), *A. pseudopunctipennis* ranges eastward into Arizona, New Mexico, and Texas. In these regions it is found principally along the valleys of the larger rivers, such as the Rio Grande and Pecos, where irrigation is practiced extensively (Barber, Komp, and King, 1929; Gerber, 1931; Barber and Forbrich, 1933; Adams, 1936; Greiner, 1936; Barber, 1939); it is also known from Oklahoma, Tennessee, Mississippi, and Louisiana. *A. pseudopunctipennis* has recently been found in Nevada: Beatty, Nye County, and Indian Springs, Clark County, May 26, 1940; Tule Springs, Clark County, May 24, 1940 (Reeves, Cazier, Ting, collectors); it also occurs in southern Utah in the vicinity of St. George, Washington County (D. M. Rees, *in litteris*).

Southward, *A. pseudopunctipennis* occurs throughout Mexico, particularly favoring the drier mountain zone back from the sea (Hoffmann, 1931, 1937). I had the opportunity of examining adults of this species from Baja California collected by A. E. Michelbacher and E. S. Ross during the summer of 1938 (Distrito del Norte: Rosarito Beach, July 5; Santo Tomás, August 3; San Fernando Mission, July 1; Punta Prieta, June 21. Distrito del Sur: 19 miles south of Mulegé, July 1; Comondú, July 21; larvae in barrel; San José del Cabo, July; Mr. Green, San José del Cabo Department of Public Health).[14] This is a further extension of its known range; except for a Tia Juana record (June 2, 1906, Dyar and Caudell, see Howard *et al.*, 1917), the only mosquitoes reported from the peninsula, so far as known to me, are *Culex quinquefasciatus* Say, *C. tarsalis* Coquillett (Martini, 1935), *Aedes aegypti* (Linn.) (Howard *et al.*, 1917), and *A. maculipennis (freeborni)* (Dyar, 1907).

A. pseudopunctipennis is found continuously through Central America to Colombia, where it spreads eastward into Venezuela and the islands of Grenada and Trinidad and southward following the Andes, through Ecuador, Peru, Bolivia, and northern Chile down into the foothill provinces of northeastern Argentina.

LARVAL BIONOMICS

BREEDING PLACES

This anopheline is a species inhabiting arid canyons and valleys, where the immature forms find ideal conditions for growth in the small, slow-moving streams (figs. 33, 34) and side pools of receding rivers containing a rich growth of green algae (*Spirogyra, Chladophora, Oedogonium*, etc.) well exposed to the sun (see Shannon *et al.*. Hoffmann and Alvarado). The relation of *A. pseudopunctipennis* to algae is well brought out by Shannon, Davis, and Del Ponte (1927, p. 693), "La distribución de las algas tiene una relación muy importante con la distribución de *pseudopunctipennis*. Nos afirmanos en nuestra opinion de que el desarrollo favorable de las larvas, depende en gran parte de la existencia de algas, por lo menos para lograr la producción de grandes cantidades de estos mosquitos. En toda la región argentina, donde se conoce *A. pseudopunctipennis*, las algas verdes constituyen una característica resaltante de los lugares de reproducción abundante."

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[14] T. H. G. Aitken, Contributions toward a knowledge of the insect fauna of Lower California. No. 6 Diptera: Culicidae. Calif. Acad. Sci. Proc. ser. 4, 1942, 24:161–170.

In California I have repeatedly observed this species in pools much too warm for *A. maculipennis (freeborni)* or *A. punctipennis;* this apparent preference of *A. pseudopunctipennis* has likewise been noted in other parts of its range (Barber

33

34

Figs. 33, 34. Breeding place of *A. pseudopunctipennis* in a side arm of Calaveras Creek, Sunol, California. Collections of adult mosquitoes were made under the bridge. The heavy growth of algae (*Zygnema* and *Chladophora*) harbors numerous larvae.

et al., 1929; Root and Andrews, 1938). On the island of Grenada the latter authors found that 50.9 per cent of the *pseudopunctipennis* breeding was in lagoons and canals and 33.3 per cent in side pools of streams. Although the larvae are frequently found associated with algae, they do occur in clear pools devoid of vegetation. I saw just such a place near Loomis, Placer County, California. Water had seeped

into sandpits left by a gold dredger; these holes, about three to four feet long, two feet wide, and about one and a half feet in depth, were quite bare of any visible vegetation or flotage and were completely exposed to the sun throughout the day, yet they supported a large population of larvae, all instars.

Along the California coast, where small creeks are unable to break through to the ocean, a small pool is frequently formed on the beach; Herms and I have on a number of occasions found *A. pseudopunctipennis* breeding in these places, usually in the presence of green algae (*Enteromorpha* and *Chladophora*); undoubtedly these pools become somewhat brackish since they are subject to the influence of extreme high tides.

In the southwestern part of the United States, Barber and others (1929, 1933) have found *A. pseudopunctipennis* abundant in the irrigated regions, particularly in New Mexico, where large areas of swampy meadows and poorly kept drains provide ideal conditions for breeding. Artificial containers such as drinking troughs may occasionally harbor larvae.

ALTITUDINAL DISTRIBUTION

This anopheline has adapted itself to varying climate over a wide vertical range. It has been collected 176 feet below sea level in the hot Coachella Valley, Riverside County (Herms, 1929), and in the Sierra Nevada at 7,300 feet in Alpine County, California (Aitken, 1939a). According to Hoffmann (1931) it may be found in Mexico from sea level up to 7,200 feet or more, and Shannon (1930) reports it in the Peruvian Andes at an elevation of 7,800 feet (Matucana).

ADULT BIONOMICS

BREEDING ACTIVITIES

I know of no observations that have been made on the mating habits of *A. pseudopunctipennis;* likewise no information has been found concerning the laboratory rearing of this species. I made various attempts to obtain mating in captivity (using the cages described in the section on *A. maculipennis*), but without success. Fertilized wild females, however, have frequently been brought into the laboratory and, following blood meals, have readily oviposited. Francisco Campos R. working with this species in Ecuador, has informed me by letter that he has kept *pseudopunctipennis* in the laboratory but as yet has never observed oviposition, despite the blood meals, and all individuals, male and female, have died within a few days.

I am inclined to believe that two forms of *A. pseudopunctipennis* occur in California, each with its particular egg type which may be found at any time of the year; they are not seasonal eggs. Interbreeding may be going on between these two forms, for transition egg batches are occasionally found in the same locality with the other two types. Moreover, and further to suggest the occurrence of interbreeding, the male progeny from atypical eggs in a locality containing both types may or may not have the ornamented phallosome.

SEASONAL INCIDENCE

My observations on the seasonal incidence of *A. pseudopunctipennis* in California have been restricted to the vicinity of Sunol. As with *A. maculipennis*, these studies were carried on from August to April. The graphs (figs. 23, 35) show a high population of males and females in August, which fell gradually during September, October, and November, and very rapidly in December, reaching a low in January and February, following which there was a sharp rise in March. The last male was

caught December 6, and a few larvae were collected as late as November 9. Females were collected occasionally during the winter in various stages of maturity, as follows: December 20, two females with blood in stomachs, fat body undeveloped and ova in stage four; December 31, two females, one with mature eggs, the other with blood in hind gut; January 3, one female, ova in stage two; January 17, one female, ovaries undeveloped, fat body developed; February 22, one female, ova in stage two. The close correlation between males and females during the early winter months, along with the above facts concerning incidence of larvae and condition of females, suggests that breeding may be going on at a very low rate during the winter months in the Coast Ranges. Additional evidence, suggesting breeding throughout the year, at least in southern California, comes in the form of one male and two females, the latter with mature ovaries, collected by W. C. Reeves in Riverside February 17, 1940.

This, however, is not the condition in which females are to be found in the central valley of California. During the winter months, only hibernating females containing immature ovaries and well-developed fat bodies have been found in these regions.

In New Mexico, Greiner (1936) reports that *A. pseudopunctipennis* probably overwinters in the adult stage. No males or females were found after the second week in October and none were reported by the third week in April when his studies were concluded; gravid females were collected as late as October 5 and larvae occurred in the breeding places until the last week in November.

Giaquinto Mira (1936) states that *A. pseudopunctipennis*, which occurs at high altitudes in Guatemala, passes the dry season primarily in the larval stage.

Elsewhere in its range, as in South America, the species does not hibernate. Shannon (1930) points out that in the dry season, except for occasional springs, it cannot survive in the lowlands and hence must resort to greatly restricted permanent water sources in the near-by mountains. With the return of the rainy season the species again reinfests the valleys. The method of migration, whether by eggs or larvae washed downstream or by flight, is not known. Nothing comparable to the dispersal flights of *A. maculipennis freeborni* has been observed for this species.

Fig. 35. The incidence of adults of *A. pseudopunctipennis* during the fall, winter, and spring of 1938–1939 at Sunol, California.

Feeding Activities

The habits of the adults of *A. pseudopunctipennis* appear to differ markedly in various regions throughout its range. The observations of Petrocchi (Mühlens *et al.*, 1925), Davis (1927), and others indicate that it is an exceedingly domestic mosquito in northwestern Argentina; Davis states that 99 per cent of the mosquitoes captured in houses in the Province of Tucumán were *pseudopunctipennis*. Other

species present were *A. argyritarsis* Robineau-Desvoidy, *A. albitarsis* Lynch Arribalzaga, and *A. tarsimaculatus* Goeldi [*A. oswaldoi* (Perryassú) ?]. The results of experiments with the preciptin reaction showed that *pseudopunctipennis* in Tucumán fed on various hosts in the following proportions: man, 50 per cent; dog, 21.8 per cent; horse, 8.9 per cent; sheep or goat, 6.2 per cent; cow, 5.5 per cent; chicken, 3.2 per cent; hog, 2.5 per cent; and cat, 1.8 per cent. "Man and dog being essentially house-dwellers at night, the results demonstrate a very high domesticity for the insect." Davis and Shannon (1928; Shannon 1930) report the same findings existing in the Peruvian Andes. In a study of the feeding habits of Venezuela anophelines, Hill (1934) found that in *pseudopunctipennis* only one out of 40 samples showed human blood. Bequaert (1938) found *pseudopunctipennis* entering houses frequently in Guatemala, where it appears to be both a diurnal and a nocturnal feeder. In Mexico, the papers of Martini (1935) and Vargas (1938) indicate that it is a very common anopheline and readily enters habitations. Precipitin tests by Vargas showed a very marked preference of *pseudopunctipennis* for human blood (67.2 per cent of 245 mosquitoes caught in houses) in Temixco, Morelos.

In the United States the habits of the adult practically reverse the condition existing in the southern and central regions of its range. Observations made in California indicate that it shows very little preference for human habitations; in this state it is rarely if ever found indoors. Herms has called it a "field mosquito" because of its usual avoidance of humans. During the 1937 survey, our party spent the night in an open tent at Lanes Redwood Flat, Mendocino County; although *A. pseudopunctipennis* was breeding extensively in the Eel River, about 50 feet from the tent, no adults were seen; whereas twice that evening *A. punctipennis* was caught trying to bite us. During the course of extensive field investigations in California I have never been bitten under natural conditions by this mosquito.

DISEASE RELATIONSHIP

Darling (1910), in Panama, was the first investigator to demonstrate that *A. pseudopunctipennis* may harbor and transmit the *Plasmodium*. He fed 4 females on a tertian carrier, obtaining no infection, but was successful in infecting 4 females out of 27 which had fed on an aestivo-autumnal case.

This species has been demonstrated conclusively to be the most dangerous vector in the Andean foothill provinces of northwestern Argentina. The results of mosquito dissections from this region are as follows (quoted from Root and Andrews, 1938): "Peterson (1911) dissected 1,549 glands of which 16 were infected, Mühlens *et al.* (1925) dissected 157 stomachs of which 2 were infected, Mazza and Gonzales (1926) dissected 28 glands of which 2 were infected, and Davis (1927) dissected 431 stomachs and 313 glands of which 11 stomachs and 3 glands were infected." More recently Del Ponte (1939) has found an oöcyst rate of 1.7 per cent among 644 females dissected in the province of Jujuy.

A. pseudopunctipennis is considered by J. Noé of Santiago to be the most important anopheline in Tacna and Arica in northern Chile (Shannon *et al.*, 1927). Epidemiological evidence gathered by Shannon (1930) indicates that this species is the mosquito of importance on the western slope of the Peruvian Andes and the chief vector at certain altitudes from 1,500 to 3,500 feet on the eastern slope. Wille (1934) reports finding *pseudopunctipennis* infected with malaria in the Covención and Lares valleys, Cuzco, Peru. Campos R. (1928, p. 19) makes this statement concerning *pseudopunctipennis* in Ecuador, "Su carácter es severamente sanguinario así como en una memorable mañana de Diciembre de 1924, denuncié

como esparcida en territorio ecuatoriano esta especie de tanta importancia en materia médica, por transmitir activamente el *Plasmodium falciparum,* esporozoario hemosporidio causante del paludismo pernicioso."

Benarroch (1928), in Venezuela, dissected 103 mosquitoes and found no infections. In that country as well as in Panama, *A. pseudopunctipennis* is not considered a vector of public health importance (Gabaldon, 1939; Simmons, 1939).

Grenada, the most southerly of the Windward Islands, is undoubtedly the type locality from which Theobald obtained his specimens of *A. pseudopunctipennis,* although he is very indefinite. During the preparation of their monograph, Howard and his co-workers had no material from this island and concluded that Theobald's locality might have been Grenada, Nicaragua; however, the recent findings of Earle (1936) and Root and Andrews (1938) suggest that the island of Grenada may have been the locality of the original specimens. Their studies also indicate that of the three anophelines occurring on the island, *A. tarsimaculatus* (var. *aquasalis* of Curry, 1932), *A. argyritarsis,* and *pseudopunctipennis,* the first appears to be the most dangerous vector of malaria, whereas *punctipennis* was the most abundant. L. Patiño-Camargo, Professor of Tropical Medicine at the University of Bogotá in Colombia, has told me that he considers *pseudopunctipennis* may possibly be a factor in malaria transmission in the mountains of Colombia between 2,600 and 4,000 feet, and Cadena (1938) found oöcyst rates of 1.4 per cent (74 females) and 0.9 per cent (108 females) along the Puerto Wilches railroad and in the Municipio de Guacari.

In the coffee-growing regions of the Guatemalan highlands *A. pseudopunctipennis* is extremely common and has been blamed for endemic malaria at Santiago de Atitlán (Bequaert, 1938, and Hoffmann, 1931). Hoffmann demonstrates that in the highlands of Mexico, where this species prevails to the exclusion of all others during the dry season, it is the dangerous vector. He later states (1936a) that the northern innocuous *franciscanus* extends down into Mexico, which may account for the fact that in some regions *pseudopunctipennis* is considered insignificant as a vector. Boyd and Earle (1939) have shown that *pseudopunctipennis* from Cuernavaca, Morelos, Mexico, is probably not a very efficient vector of *P. falciparum* (Cuernavaca strain) in the highlands of Mexico. Since malaria exists in San José del Cabo, Baja California, according to information obtained by Michelbacher and Ross from the local health officers, *pseudopunctipennis* may be the vector in this area; it was the only anopheline collected and was abundant; *A. maculipennis* (*freeborni*) was not collected south of San Fernando Mission.

Finally the observations of Barber and his associates (1929, 1933, 1939) in Texas, New Mexico, and Arizona, and Herms (1919, 1920, 1921) in California, although based largely on epidemiological evidence, rather definitely suggest that *A. pseudopunctipennis* in these regions is relatively harmless. Barber *et al.* made dissections of *A. maculipennis* (*freeborni*) and *pseudopunctipennis* from northern and southern Mexico; out of 263 *pseudopunctipennis* examined, none were positive, yet 1.4 per cent of 868 *maculipennis* (*freeborni*) were positive.

SUMMARY

With respect to its habits as well as disease-transmitting capabilities, *Anopheles pseudopunctipennis* is a highly variable mosquito throughout its range, not only morphologically but biologically. When one considers the large amount of territory occupied by this species, it is no wonder that variations should be present.

It is my opinion that the *A. pseudopunctipennis* occurring in California is different from the *pseudopunctipennis* found in more southern regions.

1) Two egg types are found in California; one is unique in this area and the other is similar to more southern forms but differs in being smaller and in having smaller floats, which are not fused down the midline.

2) None of the larvae occurring in California have "tails" on the postspiracular plates; moreover, the character of the antennal hair (no. 11) and the antepalmate hairs (no. 2) of abdominal segments IV and V appears to differ from that of the southern larvae.

3) Two terminalia types are known in California; one is unique in this area and the other resembles the more southern type in having leaflets, but they are extremely delicate and probably are not serrate.

4) The wings of the California *A. pseudopunctipennis* are quite different from those usually found in Mexico and northern South America.

5) The black-tipped palpi of California specimens are in marked contrast with the apically white palpi found in southern forms.

6) The feeding habits of the adults, their invasion of houses, and their consequent relation to malaria differ markedly in the two regions.

It appears, therefore, that *A. pseudopunctipennis* proper, which was described from Grenada, does not occur in California. The evidence thus far accumulated suggests instead that two additional forms of *pseudopunctipennis* occur in this state. Apparently they are not both subspecies because they occur together and are widely distributed throughout California. They may be distinct species or one may be merely a variety of the other. Although considerable morphological evidence points to their specific identity this evidence is in part weak and should be backed by longer series. For the present, therefore, I am inclined to regard the western *pseudopunctipennis* fauna as composed of one subspecies, *A. pseudopunctipennis franciscanus* var. *boydi*. The former is to be associated with the atypical egg type of Herms and Freeborn and the latter with the typical egg type of Herms and Frost. The finding of "transition" or intermediate eggs in localities where both types occur suggests that they interbreed. Although insufficient evidence is available at present, it may be presumed on the basis of the paratype series that *franciscanus* is to be associated with the males having the delicate leaflets on the phallosome, whereas *boydi* may be associated with males devoid of leaflets. Neither form is a malaria vector.

If these suppositions are correct, then *franciscanus* occurs in Nevada, Utah, Arizona, New Mexico, and western Texas, where it is associated with the males with delicate leaflets described by Barber, as well as with the "black-winged" individuals. The same is true of Baja California, except for the Cape region, and parts of Mexico proper.

A. pseudopunctipennis pseudopunctipennis is associated with the large egg type of Rozeboom and Vargas; the larvae have "tails"; the males have well-developed, serrated leaflets and the adults are "pale-winged" individuals and bear white-tipped palpi. It is found in Mexico and southward, and apparently invades eastern Texas and other parts of southern United States. It is a more dangerous mosquito than *franciscanus* and in some parts of its range is an active agent in malaria transmission. The *pseudopunctipennis* of South America may eventually be found to differ from that form occurring in the central part of its range.

Thus, I recognize, for the present, two subspecies and one variety of *A. pseudopunctipennis*, only the last two of which occur in California: *Anopheles pseudopunctipennis pseudopunctipennis* Theobald; *Anopheles pseudopunctipennis franciscanus* (McCracken); *Anopheles pseudopunctipennis franciscanus* var. *boydi* (Vargas).

Anopheles punctipennis (Say)

Culex punctipennis Say, 1823, 3:9.
Anopheles punctipennis Say, 1824, 2:357
Culex hyemalis Fitch, 1847, 5:281
Anopheles perplexens Ludlow, 1907, 39:267

Type locality.—"Inhabits the United States." Except for this general statement, the only specific localities mentioned by Say are the Mississippi River and the coast of Maryland.

Description.—HEAD with occiput clothed with upright, triangular scales, those on the vertex white, with black ones laterally, ocular bristles black, those between the eyes white; palpi as long as proboscis, dark brown; proboscis dark. THORAX with mesonotum with pale, pruinose gray stripe bounded laterally by dark bands, vestiture of narrow straw-colored scales, a tuft of whitish ones just posterior to head; wings with black and yellow scales, the latter forming two spots on the costal margin, one of which is large and situated beyond the middle, also including R_1 (1st vein) and R_{2+3} (2d vein), the other on the apex of costa R_1 and upper fork of R_{2+3}, lower fork of R_{2+3} with small spot, media (4th vein) with small spot on basal half, another near cross vein (m–cu) and one in middle of each fork, anal (6th) vein with spot near base; tips of femora and tibiae narrowly pale-scaled. ABDOMEN dark brown with numerous brownish hairs.

DISCUSSION

Male terminalia.—The separation of *A. punctipennis* from *A. maculipennis* on the basis of male terminalia is difficult. Frost (1932, p. 284) states, "Claspettes, bilobed, dorsal lobe small, with two closely set, short stout spines; ventral lobe much broader with an outer large, broad and sharp-pointed spine, an inner smaller spine and midway between these spines a hair." I have seen a number of terminalia preparations where there are only two stout spines on the claspette; it is this character, the presence of two or three sharply pointed spines, which Matheson (1929) uses to separate *punctipennis* from *maculipennis*. The character given by Freeborn (1926, p. 447) appears to be fairly satisfactory: "Claspette lobe abruptly conical... *punctipennis*" and "Claspette lobe rounded ... *maculipennis*."

Larvae.—The identification of the larvae of *A. punctipennis* has always been difficult. Matheson and Shannon (1923) separated *punctipennis* from *A. quadrimaculatus* on the basis of five and six pairs of palmate hairs, respectively: they distinguished *punctipennis* from *A. maculipennis* (*occidentalis*) by the lateral plate of abdominal segment VIII, which has 12–22 (6–7 long) teeth in the former and 22–29 (8–9 long) teeth in the latter.

Root (1924a) found that the number of palmate hairs was variable in both *A. punctipennis* and *A. quadrimaculatus;* however, it was noted that this hair on abdominal segment II was never pigmented in *punctipennis* and usually pigmented in *quadrimaculatus*. A more reliable character was found in the antepalmate hair (no. 2) of abdominal segments IV and V, which is normally bifurcate (basally) in *punctipennis* and single in *quadrimaculatus*.

Russell (1925) separated *A. punctipennis* from *A. quadrimaculatus* and *A. crucians* on the basis that in the first species the anterior inner clypeal hairs (no. 2), are close together and the antepalmate hairs (no. 2) of abdominal segments IV and V are usually double.

More recently Bradley (1936) has remodeled the key to the anophelines of the United States. *A. quadrimaculatus* is recognized by the "Tubercles of inner anterior clypeal hairs separated by at least the width of one of these tubercles; antepalmate hairs on segments 4 and 5 usually single, palmate tufts on segment 2 usually well developed." *A. punctipennis* is separated from *A. maculipennis* in the following dichotomy: "Antepalmate hairs of abdominal segments 4 and 5 usually with 2 branches, rarely 1 or 3; posterior clypeal hairs usually with 2 branches from near base; inner anterior clypeal hairs single, unbranched ... *punctipennis*. Antepalm-

ate hairs of abdominal segments 4 and 5 usually with 3 branches, rarely 2 or 4; posterior clypeal hairs usually long with apical branching; inner anterior clypeal hairs unbranched or with 2 to 3 branches beyond middle ... *maculipennis."* Bradley's key is probably satisfactory for the eastern *punctipennis,* but it will not separate the western *punctipennis* from *A. maculipennis freeborni.* In fact none of the existing keys adequately separate these two forms. Although only a limited amount of material has been examined, the only satisfactory character I have found is the pigmentation of the head capsule, the frontoclypeal sclerite in particular; in California *punctipennis* has a white (pale) horizontal band separating the pigmented band of the frontal hairs from the dark posterior triangle, whereas in *freeborni* the pigmentation is broken up into spots (see fig. 11). Apparently this is not true of the eastern *punctipennis,* for Matheson and Shannon write (p. 61),

"In *punctipennis* the transverse bands of the head are indistinct or lacking ..." In California, the antepalmate hairs (no. 2) of *punctipennis* on abdominal segments IV and V vary from two to three, the former possibly being the more common number; also the posterior clypeal hairs (no. 2) are predominantly bifurcate to the base.

Pupae (fig. 36).—Senevet (1930, p. 126), in his treatment of the pupae of *Anopheles,* figured and described the pupa of *A. punctipennis* from two cast skins from Illinois (in the British Museum). I have compared California material (three skins from Bridge Inn, Tulare County) with Senevet's description and find that certain differences are apparent. Hair C is single on segments V to VII in the California material, whereas in the Illinois specimens C is five-branched on V, bifurcate in one cast skin and single in the other on VI, and questionably single in both skins on VII. These differences are probably variable, and may be geographical variations. Additional material must be studied. Hair B is four-branched on V to VII. Spine 9 is $\frac{1}{5}$ the length of segments VI and VII, rather robust and somewhat blunt. Average length of paddle, $.956\mu$, average width, $.688\mu$, ratio 1.4:1.

Fig. 36. Pupal chaetotaxy of *A. punctipennis* (see fig. 3 for terminology).

The pupae of *A. punctipennis* may be separated from the American *A. maculipennis* on the basis of the branching of hairs B and C and by the fact that spine 9 on segments VI and VII is shorter and somewhat blunt. In *A. maculipennis occidentalis* hair B is: one- to four-branched (average 2.37) on segment V, one- to three-branched (average 2.14) on VI, and one- to two-branched (average 1.8) on VII; hair C is: one- to two-branched (average 1.5) on V, one- to two-branched (average 1.14) on VI, and single on VII. In *A. maculipennis freeborni* hair B is: four- to five-branched (average 4.25) on V, four- to five-branched (average 4.25) on VI, and three- to four-branched (average 3.6) on VII; hair C is: two- to five-branched (average 4.0) on V, two- to three-branched (average 2.25) on VI, and one- to two-branched (average 1.75) on VII.

Eggs (fig. 37).—In the course of these investigations I have attempted to discover if any marked variation or unbalance exists within this species. Nothing of importance has yet been found. Occasionally one finds adult specimens which have dull-colored wings; that is, the pale spots are somewhat indistinct; normally, however, the wing maculations are very clearly defined.

A great many eggs have been examined at various seasons of the year. Only once was a form found differing from the usual type (fig. 38). This was a batch of

150 eggs laid by a female caught at Sunol, February 25, 1939. Nine of these eggs are abnormal. The typical *A. punctipennis* egg as described by Herms and Frost (1932) ranges from 534μ to 578μ in length, and the "frill" extends around the periphery of the dorsal surface and is not interrupted by the floats, which have from 16 to 20 compartments. The chorion of the dorsal surface of the egg is finely granular and the ventral surface (exochorion) has a definite polygonal pattern. In these atypical eggs, the frill, instead of encircling the egg, extends posteriorly only halfway along the dorsum; as a result, the polygonally reticulated exochorion of the venter is pulled into view over the posterior dorsal surface of the egg. Furthermore, the floats are greatly elongated and sometimes almost meet at the posterior tip of the egg. The over-all length varies from 487μ to 537.5μ, the greatest
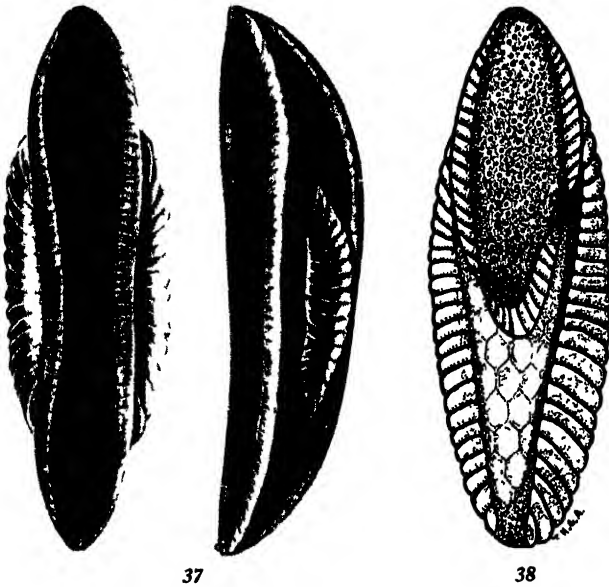
Fig. 37. Egg of *A. punctipennis* (from Herms and Frost, 1932).
Fig. 38. Egg variant of *A. punctipennis*.

width averages 175μ, the length of the frill averages 312.5μ, the length of the float averages 350μ, and the float chambers range in number from 22 to 30. Since the other eggs in the batch approach the normal type in measurements and because other females caught at the same time oviposited perfectly normal eggs, I feel that this is merely an aberrant batch of eggs. This emphasizes the importance of studying large amounts of material.

Recently, Lawlor (1940) has described an "unusual" type of *A. punctipennis* egg from Magnolia Springs, Jenkins County, Georgia. It is believed that these are "seasonal" eggs since they were obtained during January and February, and as summer approached they gradually decreased in numbers in favor of the "usual" egg type. The new eggs are characterized by the exochorion, which completely covers the dorsal surface except for a dark oval area of exposed chorion at the poles; moreover, the polygonal reticulation of the exochorion on the ventral surface is hardly visible on the dorsal surface or "deck." No difference in size or number of float chambers was noted between the "usual" and "unusual" eggs, such as may be found in *A. walkeri*. Lawlor further indicates that differences appear to exist

between the eggs of the "usual" type of the East and those occurring in California in the total length, frill, float length, and the number of float compartments.

The number of eggs laid by this species appears to vary considerably; oviposition records in this laboratory indicate an average slightly in excess of 200, with a maximum of 352; I once observed one female oviposit over a three-week period a total of 500 eggs (166, 145, 154, 35).

DISTRIBUTION

A. punctipennis is one of the most widely distributed anophelines in North America, being found abundantly from southern Canada down the Atlantic seaboard and the Mississippi Valley, southward through eastern Texas, also in eastern New Mexico (Pecos River Valley), and extending into Mexico as far south as the states of Guanajuato and Hidalgo, approximately 21 degrees north latitude (Howard *et al.*, 1917; Hoffmann, 1937). West of the Divide, it ranges from British Columbia (Duncans, 50° N. lat., cited by Howard *et al.*, 1917) down through Washington (Hatch, 1938) and Oregon (Stage and Gjullin, 1935; Stage, 1938) to the Tehachapi Mountains in southern California; there is one record south of the Tehachapi at Bonsall, San Diego County (see Herms, 1929, fig. 2), but this is extremely doubtful because the only specimens from that locality in the University of California collection are *A. pseudopunctipennis*. Montana is the only other western state reporting the presence of this species; Mail (1934) cites a single record from the Bitter Root Valley. Its distribution north and south is thus seen to cover roughly 30° latitude. In California *punctipennis* is scattered widely throughout the central and northern parts of the state, but reaches its peak of development along the Sierra foothills of the Mother Lode region as well as along the shaded water courses of the Sacramento and San Joaquin valleys.

LARVAL BIONOMICS

This species appears to be primarily a shade lover, breeding in pools of clear, cool water which are usually to be found in the beds of wooded creeks that are slowly drying up; green algae are frequently a constituent of these pools. In the eastern United States Matheson (1929) reports he has "found the larvae in nearly all aquatic situations except leafy pools in densely wooded areas." This slight difference in major breeding preference may be an adaptation to the warmer and dryer climate of California; in the Northwest the larval habitat appears even less constant, resembling more that of the East. Investigations of the United States Public Health Service indicate that *A. punctipennis* does not tolerate brackish or salt waters (Griffitts, 1921).

ADULT BIONOMICS

In reference to the overwintering habits of this species in California, I made a number of observations at Sunol from July 29, 1938 to May 1, 1939. Adults were found throughout the winter and were particularly prevalent in the months of November and December. An examination of the graphs (figs. 23, 39) shows the marked rise in females in November with a corresponding slight rise in males during the same period, which suggests that this may be a late fall species; a low was reached in January following which there was another marked rise with the advent of spring. Dissections of the adults, some of which contained blood, during this period indicated a variation in the degree of development of the ovaries and the fat body; eggs were obtained frequently in the laboratory, and a few larvae were found at all seasons. Thus it is suggested that along the coast *punctipennis* continues to breed and develop slowly throughout the winter.

The observations of Griffitts (1919) in the East and South indicate that this species may overwinter in the larval, as well as the adult stage (Boyd and Weathersbee, 1929) and occasionally even emergences take place in the winter (Barber, Komp and Hayne, 1924; Balfour, 1928).

I made a trip through the northern San Joaquin Valley in the middle of December in an effort to find anopheline breeding places, but I was unable to find larvae, thus substantiating the earlier observations of Herms (1929) and Freeborn (1926). During the winter there are few suitable breeding places available in the interior valleys; the foothills offer better opportunities, but no larvae were observed. Hibernating adults of *A. punctipennis, A. maculipennis freeborni,* and *A. pseudopunctipennis* were collected in a number of places; these were dissected and in all of them the ovaries were immature and the fat body was well developed.

No spring or fall dispersal flights, characteristic of *A. maculipennis freeborni,* have been observed for this species.

Rearing of *A. punctipennis* in the laboratory has been successfully accomplished by Boyd and Mulrennan (1934), who report the establishment of a cage colony of this species which had at that time passed through three generations. Differences were noted in the feeding activities of *punctipennis* as compared with *A. quadrimaculatus;* the former will attack a Negro more avidly than it will a white person; *punctipennis* appears to show a preference for the upper parts of the body, whereas *quadrimaculatus* generally attacks the legs. No mention is made of swarming of the males. Swarming of *punctipennis* was first reported by Knab (1907). Copulation is effected in flight; the grappling pairs, falling out of the swarm, join and then drift to the ground.

Fig. 39. The incidence of adults of *A. punctipennis* during the fall, winter, and spring of 1938–1939 at Sunol, California.

DISEASE RELATIONSHIP

The susceptibility of this species to *Plasmodium vivax* (Grassi and Feletti) and *P. falciparum* (Welch) has been demonstrated by King (1915, 1916a, 1916b), Mayne (1916, 1917), Barber, Komp, and Hayne (1927), Boyd and Kitchen (1936), and many others, but as a major vector of malaria, it is considered a species of minor importance. There is some thought that *A. punctipennis* may be responsible for some of the malaria in the Mother Lode region of the Sierra Nevada of California, a region where this species is particularly abundant. The observations of Herms (1921) and others in California indicate that *punctipennis* is to be considered a so-called "porch mosquito," because it does not readily enter houses.

RÉSUMÉ OF THE ANOPHELINE COMPLEX IN
WESTERN AMERICA

As a result of these studies, the following mosquitoes are considered as comprising the anopheline fauna of western America: *Anopheles maculipennis occidentalis, A. maculipennis freeborni, A. pseudopunctipennis franciscanus, A. pseudopunctipennis franciscanus* var. *boydi,* and *A. punctipennis.*

A. maculipennis occidentalis occurs in a narrow strip along the coast from Ventura, California, northward, swinging eastward into Idaho and Montana. *A. maculipennis freeborni* occurs throughout the Great Basin area and in the central valleys of California, Oregon, and Washington. *A. pseudopunctipennis franciscanus* var. *boydi* appears to be restricted to California. *A. pseudopunctipennis franciscanus* is distributed throughout California, Arizona, and New Mexico and through part of Nevada, Utah and Texas. *A. punctipennis* is found in the central valleys of Washington, Oregon, and California, as well as in the Pecos River Valley in New Mexico and the Bitter Root Valley in Montana.

In disease transmission *A. maculipennis freeborni* is the most important, if not the only vector of malaria in the West, particularly in the irrigated regions of New Mexico, and in the San Joaquin and Sacramento valleys in California, and in the Willamette Valley in Oregon.

As a result of this investigation a number of additional problems have presented themselves. More information should be obtained, for instance, concerning the food requirements and salt tolerance of larvae. The recent work of Bates (1939*a*) on the use of salt solution for demonstrating physiological differences between larvae of different species and subspecies or varieties could be well applied to western anophelines. The establishment of laboratory colonies should be undertaken with the object in mind of carrying on interbreeding experiments between such closely related forms as *occidentalis* and *freeborni*, or *franciscanus* and *boydi*. If copulation cannot be effected, for instance, between *occidentalis* and *freeborni*, perhaps the males of *aztecus*, which readily mate in captivity, could be employed, just as the stenogamic *atroparvus* of Europe has been used successfully in interbreeding experiments with other eurygamic forms of the European *maculipennis* complex. The use of colored lights to stimulate swarming, as discussed by Bates and Hackett (1939), might also be of value in attempting to establish laboratory colonies as well as to carry on interbreeding experiments. The true relationship of *franciscanus* and *boydi* with each other and with the *pseudopunctipennis* of Mexico should be investigated more thoroughly. Finally, I believe that some attempt should be made to determine the susceptibility of the various western anophelines to plasmodial infection, since our present knowledge of this subject is almost entirely epidemiological.

ADDENDUM

Subsequent to submitting this paper for publication several new names have been published by Vargas for variants noted in the American anopheline complexes. Although I have not had the opportunity of carefully studying these new forms, I mention them here for completeness.

Anopheles pseudopunctipennis var. *willardi* Vargas [1941, Bull. Brooklyn Ent. Soc., 36(2):73–74] was described from Ciudad Juárez, Chihuahua on the basis of a slight difference in the egg, the distance of the float structure from the frill-like collar being about half way between the measurements found in typical *pseudopunctipennis* and *franciscanus.* This appears to be merely a variation of minor importance which in a long series would probably break down.

Anopheles punctipennis stonei Vargas [1941, Rev. Soc. Mex. Hist. Nat., 2(2–3) : 175–186] was proposed for a predominantly southern form of this species having a black body clothed with white hairs in contrast to the typical form having a light brown body and yellow hairs; in addition the larvae are said to differ in the degree of branching of the outer clypeal hairs. The type locality for *stonei* is Monterrey, Mexico, and is also reported from California, Alabama and Canada; typical *punctipennis* specimens were seen from Canada, New York, Washington, D. C., Virginia, South Carolina, Alabama and Louisiana. In the same paper Ludlow's old name *perplexens* was reinstated for the individuals having reduced wing spots. Nowhere in the United States has this type been found as a group, except at Rock Springs, Florida (King, Bradley, and McNeel, 1939, 1942), which suggests that the *perplexens* form is merely a melanic variant common among many animals.

Anopheles earlei Vargas [1943, Bol. Officina Sanit. Panamericana, 22(1) :8–12] has recently been proposed for the *Anopheles maculipennis occidentalis* east of the Rocky Mountains (type locality: Jefferson County, Wisconsin). The difference is described as lying in the processes of the ninth tergites of the male terminalia, which in *earlei* are short and wide, whereas in *occidentalis* they are long and slightly dilated apically. Alan Stone informs me that males in the type series of *occidentalis* from Stanford University demonstrate a complete range of variation in the distinguishing character. Obviously, if no better means of recognition can be found, *earlei* as a specific or subspecific entity cannot exist.

T. H. G. A.

Florida, Aug. 31, 1943

APPENDIX

Listed below are records of the "silver-tipped" *A. maculipennis occidentalis* in North America, based upon specimens in the National Museum, at the University of California, Stanford University, Montana State College, and the University of Minnesota, as well as specimens listed by Mail (1934 and *in litteris*), Matheson and Shannon (1923), Hearle (1927), Lathrop (1939), and Dr. W. V. King and J. A. Rowe (*in litteris*):

CALIFORNIA. *Ventura County:* Ventura, July 21, 1917, W. B. Herms and S. B. Freeborn. *San Luis Obispo County:* San Luis Obispo, Sept. 2, 1919, W. B. Herms and S. B. Freeborn; Harmony, Cayucos, San Simeon, and Pico Creek, Sept. 25, 1938, T. Aitken and M. Cazier. *Monterey County:* Prewitt Creek, Sept. 25, 1938, T. Aitken and M. Cazier; Carmel, July 7, 1938, T. Aitken; Asilomar, June 1, 1920, W. B. Herms; Monterey and Castroville, Oct. 22, 1937, T. Aitken; Salinas, Aug. 16, 1917, W. B. Herms and S. B. Freeborn. *Santa Cruz County:* Twin Lakes, Aug. 10, 1937, W. B. Herms, D. Howell, and T. Aitken; Santa Cruz, Aug. 16, 1917, Herms and Freeborn. *San Benito County:* Ausaymas School near Hollister, June 27, 1940, S. Dommes; Dunnville, July 7, 1940, Aitken and Cazier; San Juan Bautista, July 18, 1917, Herms and Freeborn. *San Mateo County:* Sharps Park and Pescadero, Aug. 10, 1937, Herms, Howell, and Aitken. *Santa Clara County:* San Jose, July 28, 1906; Milpitas, July 18, 1917, Herms and Freeborn; Saratoga, Aug. 15, 1917, Herms and Freeborn; Stanford University, 1903, I. McCracken. *San Francisco County:* San Francisco, Nov. 28, 1919, E. P. Van Duzee, California Academy of Sciences. *Alameda County:* Oakland, July 27, 1903. *Contra Costa County:* Crockett, Aug. 24, 1917, W. B. Herms and S. B. Freeborn. *Solano County:* Mare Island, July 14, 1916, W. B. Herms and S. B. Freeborn. *Marin County:* Ignacio, July 27, 1916, W. B. Herms; Point Reyes Station, March 19, 1939, T. Aitken; Fallon Junction, Aug. 13, 1937, Herms, Howell, and Aitken. *Sonoma County:* Petaluma, July 27, 1916, W. B. Herms; Sebastopol, July 9, 1939, T. Aitken; Valley Ford and Bodega, Aug. 14, 1937, Herms, Howell, and Aitken. *Mendocino County:* Fort Bragg and Ten Mile River, Aug. 14, 1937, Herms, Howell, and Aitken. *Humboldt County:* Beatrice, Aug. 6, 1916, Herms and Freeborn; Eureka, July 21, 1937, Herms, Howell, and Aitken; and probably Rio Dell, Freshwater, Fernbridge, Ferndale, and Fortuna, July 21, 1937, Herms, Howell, and Aitken. *Del Norte County:* Wonderland Park, July 20, 1937, Herms, Howell, and Aitken; Crescent City, June 16, 1939, Aitken.

OREGON. *Multnomah County:* Portland, R. P. Currie.

WASHINGTON. *Watcom County:* Lake Watcom, H. G. Dyar.

BRITISH COLUMBIA. Cranbrook, May 7, 1920; Revelstoke, Aug. 14, 1903, H. G. Dyar; Pemberton, July 21, 1929, E. Hearle; Hatzic, Aug. 5, 1921, E. Hearle; Cultus Lake, July 3, 1919, E. Hearle; Oliver, April 12, 1923, C. B. Garrett; Nicola, July 17, 1931, T. K. Molliet; Kamloops, June 7, 1931, E. Hearle; Mission, July 22, 1919, E. Hearle; Nicomen Island, June 23, 1919, E. Hearle; Chilliwack, July 3, 1919, E. Hearle; Kelowna, 1923, E. Hearle; Keremeos, 1914, S. Hadwen; Summerland, Aug., 1920, E. Hearle; Chilcotin, Aug., 1921, E. R. Buckell.

YUKON. Hootalinqua, July 6, 1919, H. G. Dyar; Valley of the Mayo River, lat. 63° 45′, long. 136°, 1904, J. Keele.

ALASKA. Anchorage, June 14, 1925, Sgt. Beroen; Fort Gibbon, June 6, 1907, through C. S. Ludlow; Gilmore, summer, 1931, G. S. Tulloch.

CANADIAN NORTHWEST TERRITORIES. Aklavik, June 5, 1931, O. Bryant; Fort McPherson, 1920, Doyle.

ALBERTA. Bilby, July 3, 1924, O. Bryant; Banff, May 21, 1924, E. Hearle.

IDAHO. *Kootenai County:* Coeur d'Alene, Aug. 19, 1931, E. Hearle.

MONTANA. *Ravalli County:* Florence, June 29, 1914, H. P. Wood; Victor, July 12, 1918, R. R. Parker. *Missoula County:* Missoula, June 24, 1914, R. A. Cooley. *Lewis and Clark County:* Helena, G. A. Mail, Glasoil, April 12, 1932. *Gallatin County:* Manhattan, April 28, 1919, G. A. Mail. *Glacier County:* North Fork Ranger Station, Glacier National Park, July 3, 1924, H. G. Dyar. *Blaine County:* Chinook, Aug. 3, 1927. *Phillips County:* G. A. Mail. *Valley County:* Glasgow, July 11, 1921. *Powder River County:* Powderville, April 21, 1916.

SASKATCHEWAN. Indian Head, Oct. 12, 1927, E. Hearle. Moose Mountains, June 26–29, 1927, E. Hearle.

NORTH DAKOTA. *Pembina County:* Pembina, May 10, 1922.

MANITOBA. Awene, April 16, 1915, N. Criddle; Winnipeg, June 1, 1922; Whitemouth, May 5, 1922.

MINNESOTA. *Roseau County:* Warroad, May 28, 1922, H. G. Dyar; Badger, June 12, 1934, W. B. Owen. *Ramsey County:* St. Paul, July 1, 1932, W. B. Owen; Minneapolis, Aug. 7, 1932,

W. B. Owen. *Chisago County:* Rush City, July 16, 1932, W. B. Owen; Taylors Falls, Aug. 5, 1922, W. B. Owen; Harris, June 25, 1933, W. B. Owen. *Aitkin County:* Aitkin, July 19, 1932, W. B. Owen. *Carlton County:* J. Cook State Park, July 18, 1932, W. B. Owen; Carlton, July 2, 1934, W. B. Owen. *Mahnomen County:* Mahnomen, July 29, 1932, W. B. Owen. *St. Louis County:* Buyck, June 17, 1933, W. B. Owen; Floodwood, Aug. 12, 1933, W. B. Owen. *Cass County:* Cass Lake, June 28, 1933, W. B. Owen; Walker, June 1, 1934, W. B. Owen. *Winona County:* Winona, July 7, 1933, W. B. Owen. *Washington County:* Stillwater, July 15, 1933, W. B. Owen. *Itasca County:* Swann River, Aug. 12, 1933, W. B. Owen; Wàrba, Aug. 12, 1933, W. B. Owen; Black Duck, Aug. 12, 1933, W. B. Owen. *Stearns County:* Sauk Center, Aug. 13, 1933, W. B. Owen. *Clearwater County:* Itasca State Park, July 30, 1932, W. B. Owen. *Lake County:* Basswood Lake, May 18, 1903, W. B. Owen. *Kittson County:* Crookston, Aug. 11, 1935, W. B. Owen. *Marshall County:* Middle River, July 25, 1935, W. B. Owen.

NEBRASKA. *Sioux County:* Glen, Aug. 1906, M. H. Swenk.

IOWA. *Allamakee County:* Wexford, 1940, J. A. Rowe. *Scott County:* Le Claire, 1940, J. A. Rowe. *Osceola County:* Allendorf, 1940, J. A. Rowe. *Blackhawk County:* Blackhawk Lake, 1940, J. A. Rowe. *Polk County:* Des Moines, 1940, J. A. Rowe. *Muscatine County:* South Fruitland, 1940, J. A. Rowe. *Butler County:* New Hartford, 1940, J. A. Rowe.

WISCONSIN. *Vilas County:* Starlake, May 4, 1934.

MICHIGAN. *Schoolcraft County:* Germfask, May 3, 1934. *Cheboygan County:* Douglas Lake, 1923, R. Matheson and R. C. Shannon. *Emmet, Genesee, Ingham, Kent, Midland, Presque, Washtenaw, Wayne,* and *Wexford counties:* W. H. Irwin.

ONTARIO. Ottawa, Sept. 3, 1908, J. Fletcher; Ottawa South, April 28, 1924, C. R. Twinn; Little Current River, July 18, 1903, W. J. Wilson; Nagogami River, June 7, 1903, W. J. Wilson; Kenora, July 2, 1918, H. G. Dyar.

QUEBEC. Mirrigau River, 1926; Gatineau Point, April 23, 1925, C. R. Twinn.

MAINE. *Aroostook County:* May 25–30, 1938, G. W. Simpson. *Franklin County:* Weld, July 25, 1910, H. G. Dyar. *Penobscot County:* Norcross, July 14, Mrs. H. G. Dyar.

NEW HAMPSHIRE. *Belknap County:* Center Harbor, Aug. 1. *Cheshire County:* East Jaffrey, May 4, 1934; Dublin, June 27, 1909.

NEW YORK. *Franklin County:* Racquette River near Buttermilk Falls, 1923, Matheson and Shannon. *Essex County:* Raybrook, 1923, Matheson and Shannon.

MASSACHUSETTS. *Franklin County:* Leverett, Oct. 8, 1923, S. B. Freeborn.

CONNECTICUT. *Tolland County:* Stafford Springs, June 7, 1934.

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A GENERIC CLASSIFICATION OF CALIFORNIA APHIDS BY MEANS OF FIRST INSTAR NYMPHS

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INTRODUCTION

INTEREST IN the immature forms of insects has steadily grown during the last few years. A glance through the literature reveals work on the various families of the Coleoptera, Diptera, Lepidoptera, Hymenoptera, and other orders. But the literature has also shown that there has been very little research on the members of the hemipterous family Aphididae. This fact has prompted me to compile the results of part of my extensive investigations into the immature forms of aphids.

This paper is a study of the first instar nymphs of many California genera of aphids, and is not to be considered revisional or monographic in scope, but rather an attempt to define certain genera in terms of the first instar so that other entomologists may have a foundation, however limited, upon which to build in connection with further phylogenetic and taxonomic research.

The keys have been based entirely upon the first instar nymph. This has not always been easy to do because of the absence of certain valuable adult characters, such as the secondary sensoria of the antennae, the wings, and the cauda.

As a matter of convenience the scope of this paper is limited to the family Aphididae as conceived by early aphidologists and to the available species occurring in or near California. In general, the information gained from a study of these species may be applied elsewhere, since many of the genera found in California are widely spread throughout the country and the temperate zone. First instar nymphs of the summer viviparae only have been studied. Nymphs of the fundatrigeniae and fundatrices have not been readily available.

ACKNOWLEDGMENTS

REVIEW OF PREVIOUS WORK

The lack of comprehensive descriptions and drawings of nymphs of the first instar aphids in the literature has been a handicap in the pursuit of this

study.[1] Most papers dealing with life histories or descriptions of new species contain only vague descriptions and drawings of the immature forms.

The earliest work wherein is found a good description and drawing of first instar nymphs was that by Pergande (1901), in which he describes and figures the first instar nymphs of *Hamamelistes spinosus* Shimer and *Hormaphis hamamelidis* (Fitch).

Excellent drawings and descriptions were furnished by Essig (1909, 1911), for the first instar nymphs of *Essigella californica* (Essig), *Trifidaphis radicicola* (Essig), and *Prociphilus fraxini-dipetalae* (Essig).

Smulyan (1918) was apparently the first person to utilize first instar nymphs in a taxonomic way. He separated three species of the genus *Aphis* occurring on apples by means of first instar stem-mothers.

Baerg (1922) used first instar nymphs to separate two species of the genus *Capitophorus* inhabiting strawberry plants.

Takahashi (1924a) published an article entitled "On the Nymphs of the Aphidinae," which was republished a short time later (1924b). Takahashi dealt with certain general and specific characters of the nymphs of the first instar of various genera, and his are the most important publications on the subject to date.

In 1928 Marchal gave good descriptions and drawings of *Eriosoma lanigerum* (Hausemann). In 1933 he described and figured the first instar nymphs of *Eriosoma lanuginosum* (Hartig), *E. ulmi* (Gmelin), *Tetraneura ulmi* Hartig), *T. caerulescens* (Passerini), and *Neorhizobius ulmiphilus* (Del Guercio).

Jancke (1930) described and figured the various forms and stages of *Eriosoma lanigerum* (Hausmann).

Börner, in 1930, brought out his "Beiträge zu einem neuen System der Blattläuse." This is the first work in which the results of examinations of the nymphs of various genera have been incorporated within a taxonomic system.

Börner opposed the use of characters occurring in the adult stage only. He held that certain characters found in the nymphs, and often in the adults as well, were in many ways better adapted for the separation of genera than the characters used up to that time. Setological characters, the kind of primary sensoria, the number of facets in the eyes, the size and shape of the cornicles were among the points emphasized.

I do not agree with Börner's tendency toward generic separation on the basis of minute differences; most of those upon which he has seized make for specific differentiation. Nonetheless, it is recognized that Börner's work is a step toward the utilization of new characters and the employment of generic characters of first instar nymphs as a check against adult generic characters.

Brues and Melander (1932) used Börner's work as a basis for the keys on the Aphididae in their "Classification of Insects."

Drews (1941) incorporated a description of the first instar nymph in the diagnosis of his new genus *Nevadaphis*.

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[1] Other works which contain some information are those of Kessler (1879–1880), Matheson (1919), and Smith (1923).

GENERAL EXTERNAL MORPHOLOGY

The most important structures of first instar nymphs, particularly from a taxonomic viewpoint, are the segmental appendages, hairs and bristles, and cornicles. The whole form shows a remarkable likeness to that of the mature apterous, viviparous female. This similarity is shown in figures 1 and 2.
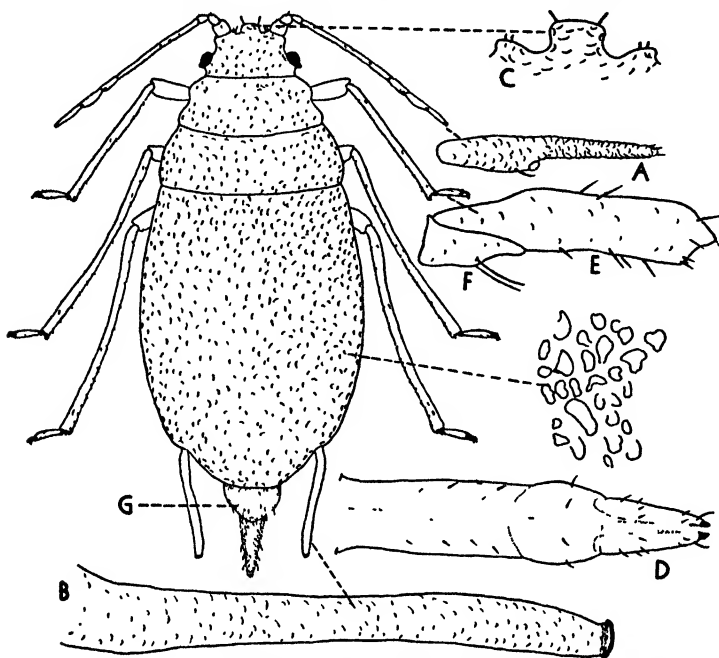
Fig. 1. *Myzaphis rosarum* (Kaltenbach). Mature apterous viviparous female.

EXPLANATION OF FIGURES

(Letters used in figures throughout have the following significations.)

A = Terminal antennal segment.
B = Cornicle.
C = Front of head.
D = Rostrum.
E = Second tarsal segment.
F = First tarsal segment.
G = Anal plate.
H = First antennal segment.
I = Dorsal tubercle.
J = Eye with ocular tubercle.

The head is only slightly narrower than the thorax. In the members of some genera, not represented in the aphid fauna of California, the head may be fused to the thorax. A suture or faint line appears to divide the head of many species; this character has not been greatly used in taxonomy because it is hard to demonstrate. The front of the head, that is, the anterior margin of the head lying between the basal segments of the antennae, is variously shaped. The vertex, or the center of the front of the head, is occasionally produced. The

frontal tubercles, situated near the bases of the antennae, are, in some species, conspicuous conical or fingerlike structures projecting from the anterior margin of the head. In most species these tubercles are absent or only faintly developed. In nearly all species there are bristles or hairs on the head the amount and arrangement of which vary. In the majority of species there are two bristles or hairs on the front.

The antennae are simple structures, rarely extending beyond the caudal end of the abdomen. For all their simplicity they are important taxonomic characters. The usual number of antennal segments is four; five segments
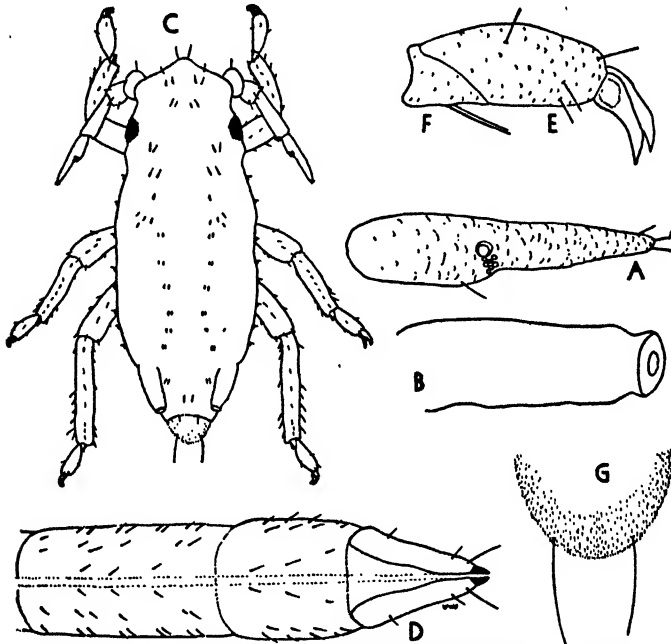
Fig. 2. *Mysaphis rosarum* (Kaltenbach). First instar nymph.

occur occasionally. Three-segmented antennae occur in two genera in California (*Chromaphis, Thoracaphis*). In these the two distal segments are fused and there are two distinct primary sensoria; the line of fusion is not visible. The terminal antennal segment bears a primary sensorium some distance away from its proximal end. This sensorium may be round, oval, transversely elongated, and tuberculate or ciliate. In all species examined there occurs near the primary sensorium a group of small circular sensoria known as marginal sensoria. All that part of the terminal antennal segment lying distally beyond the anterior edge of the primary sensorium is known as the spur; the part posterior to the anterior edge of the sensorium is called the base. In many species of the subfamily Aphididae the spur is a long whiplike extension whereas in other species of the same subfamily it is short and stubby; this is true in general for members of the subfamilies Mindarinae, Pemphiginae, and Hormaphidinae. The anterior margin of the first antennal segment in a few species is extended forward as the antennal tubercle. The first and second

segments are short, both being nearly of the same length. It may be noted here that in further growth it is the third antennal segment that divides and adds to the number of segments. The number and length of hairs on the antennal segments vary greatly.

Eyes in the first instar nymph may be compound, that is, with ten or more facets, or reduced, being then composed of three facets. The California members of the subfamily Aphidinae, so far as known, have compound eyes; but the members of the subfamilies Mindarinae, Pemphiginae, and Hormaphidinae have reduced eyes. Ocular tubercles, small faceted protuberances on the lower edge of the eyes, are absent in most species.

The rostrum is large in proportion to the rest of the body and often extends beyond the caudal part of the body. The distal segment is small, in some species indistinct and difficult to see. The succeeding segments are large and easily visible. The shape of the rostrum may be obtuse; that is, when the distal segment is short and the tip rounded; or acute when the distal segment is long and thin. The setation of the rostrum apparently has only slight taxonomic value. Few setae of variable lengths are found. Two long setae generally occur on the tip of the segment behind the small apical segment.

The thorax exhibits an evident simplicity of structure—no sclerites are visible. A few setae appear here. Lateral tubercles, small simple projections, are often present.

The legs, in a few species, are long and large in proportion to the body; the majority of species show no disproportion in this respect. The legs are similar to adult legs in their structure and are composed of the following segments; coxa, trochanter, femur, tibia, and tarsus. The tibia is the longest of the segments; it often bears longer hairs than those on other leg segments. The tarsus is composed of two small segments, the second, or terminal, segment of which bears the claws. In the fauna outside of California there exist aphids in which the tarsi are absent or composed of one segment, but unfortunately nothing is known of these aphids in the first instar. The first tarsal segment is small and, when viewed from the side, is approximately triangular. The second segment is larger than the first and more elongated. Setae occur on most segments of the legs, those on the tibia having a characteristic arrangement in some groups of aphids. Further study is needed to indicate whether the value of the arrangement is generic or specific. The first tarsal segment of the first instar nymphs of California aphids, except for members of the genera *Pterochlorus, Forda,* and *Trifidaphis,* bears two setae of variable length; the segment bears four or more setae in the genera mentioned above. The second segment bears a variable number of setae of varying lengths.

The abdomen is simple in form and varies only slightly from the usual ovate shape. There are eight abdominal segments. Lateral tubercles are often present, but dorsal tubercles are rarely seen. In members of the genus *Cavariella* a single tubercle is found on the dorsum of the last abdominal segment. The cornicles are located on the sixth segment; they may be absent in some species. These structures vary in form from mere pores to long tubular projections. They are not reticulated but they may be slightly imbricated in some

species. The anal plate is generally rounded and wider than long although in a few species it is nearly triangular. It may bear two or more setae and be highly setulose. The cauda is absent. Wax pores are well developed in some species but are difficult to find.

Dorsal setation of the abdomen offers valuable taxonomic possibilities. Hairs may occur along the margin of the body from the last abdominal segment to the eyes, as well as down the center of the body from the cauda to the front of the head. The hairs are arranged so that there are longitudinal and transverse rows. Only the two marginal rows may be present, but generally there are four or six longitudinal rows. These hairs may be simple or capitate. In some species the hairs are very numerous, making it impossible to see their exact arrangement.

These nymphal characters are of potential value in indicating the phylogeny of various groups and their relationship to one another, and a thorough study of first instar nymphs may result in clearing up the status and position of many genera and species of aphids.

CLASSIFICATION OF FIRST INSTAR NYMPHS
Family APHIDIDAE (Latreille 1802) Harris 1841

Head with front flat or rounded, occasionally with frontal tubercles. Antennae typically four-segmented, occasionally five-, rarely three-segmented; spur of terminal segment always present; primary sensoria present, one each, on the two distal segments; oval, subcircular, or transverse in shape, usually with a number of marginal sensoria near the primary sensorium of the terminal segment. Eyes three-faceted or compound; ocular tubercles rarely present. Rostrum obtuse or acute, often projecting beyond caudal end of body. Thorax simple. Legs of normal type. Cornicles present or absent; when present, ranging in form from pores to slender tubular prolongations. Anal plate usually wider than long. Cauda absent.

Börner (1930) divided the family Aphididae, as then understood, into two families: Aphididae and Eriosomatidae (Pemphigidae). This was done on the basis of adults. But it is impossible on the basis of the first instar nymphs at hand to find any major differences to uphold this separation. Börner gave no nymphal characters to back up this classification, although at times he used nymphal characters in the higher categories of his system.

Similarly, there are no clear-cut characters separating the nymphs of the four subfamilies recognized by Baker (1920). The first instar nymphs of all subfamilies resemble one another greatly, so greatly in fact that it is difficult to find even key charters to separate them.

For convenience the classification of Baker (1920), and in part that of Oestlund (1918, 1920), has been followed.

<div align="center">KEY TO SUBFAMILIES OF THE APHIDIDAE</div>

1. Eyes compound..Aphidinae
   Eyes three-faceted..2
2. Head not wider than long..Mindarinae
   Head wider than long..3

3. Two long slightly capitate hairs on dorsum of second tarsal segment.....Hormaphidinae
The two slightly capitate hairs absent from dorsum of second tarsal
segment...Pemphiginae

Subfamily Aphidinae Buckton 1876

Head with front flat or rounded; frontal tubercles often present. Spur of terminal antennal segment usually long and thin; base with oval or subcircular primary sensorium. Eyes compound. Cornicles varying from hemispherical to triangular in shape. Setae on first segment of fore tarsus typically two in number; rarely more.

KEY TO TRIBES OF THE APHIDINAE

1. Cornicles absent..Fullawayini
Cornicles present 2
2. Vertex greatly produced, trapezoidal................................Saltusaphidini
Vertex faintly produced, flat or rounded................................3
3. Dorsal abdominal setation of twelve or more hairs or bristles; when setation twelve,
spur of terminal antennal segment shorter than base......................Lachnini
Dorsal abdominal setation of twelve or less hairs or bristles; when setation twelve,
spur of terminal antennal segment longer than base............................4
4. Cornicles longer than wide; if porelike, abdominal pleural hairs short..........Aphidini
Cornicles as long as or shorter than wide; if longer, hairs on antennae long; if porelike,
abdominal pleural hairs long.......................................Callipterini

Tribe Lachnini Thomas 1879

Head with front rounded; frontal tubercles absent. Antennae typically four-segmented and bearing long hairs. Cornicles on distinct cones or swellings. Dorsal abdominal setation of twelve or more hairs or bristles. First segment of fore tarsus bearing two setae, occasionally more.

Börner (1930, p. 122) stated that in members of his subfamily Cinarinae, the equivalent of the tribe Lachnini here, four setae occurred on the first tarsal segment of the first instar nymph. This is incorrect. Of the four genera placed there by him, *Lachnus, Essigella,* and *Schizolachnus* have two setae; *Pterochlorus* has twelve setae.

KEY TO SUBTRIBES OF THE LACHNINI

1. First segment of fore tarsus with two setae....................................2
First segment of fore tarsus with twelve setae..........................Pterochlorina
2. Dorsal abdominal setation of long hairs..................................Lachnina
Dorsal abdominal setation of twelve bristles............................Eulachnina

Subtribe *Eulachnina* Baker 1920

The characters of the subtribe in the only genus known to occur in California are indicated below.

Genus **Essigella** del Guercio 1909
(Fig. 3)

Body small, elongate and narrow, comparatively parallel-sided, hairs inconspicuous. Head longer than wide; front rounded, with four slightly capitate setae. Antennae four-segmented, bearing a few short hairs; terminal segment
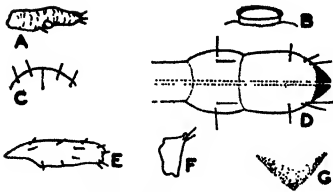
Fig. 3. Genus *Essigella.*
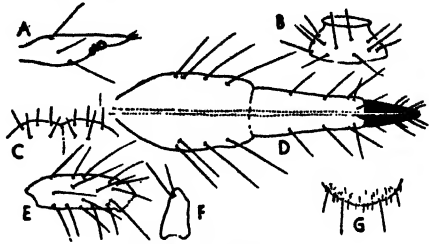
Fig. 4. Genus *Lachnus.*
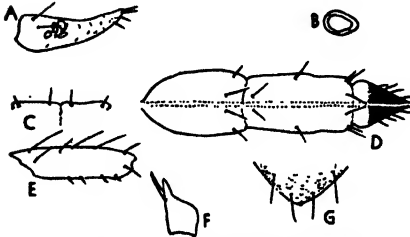
Fig. 5. Genus *Schisolachnus.*
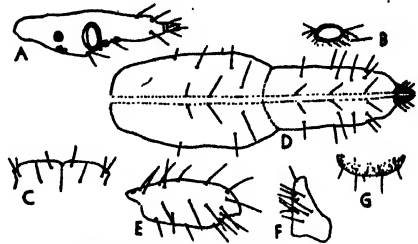
Fig. 6. Genus *Pterochlorus.*
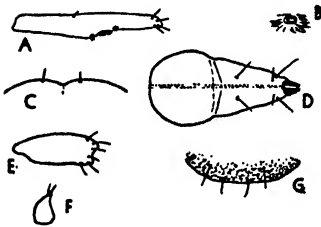
Fig. 7. Genus *Phyllaphis.*
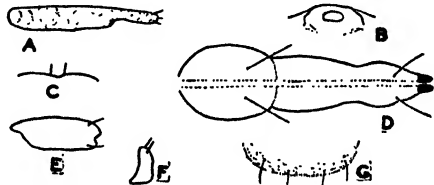
Fig. 8. Genus *Stegophylla.*
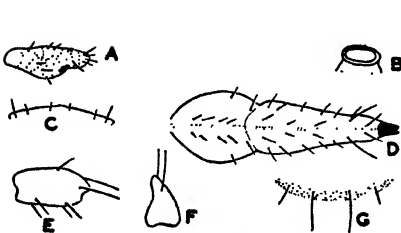
Fig. 9. Genus *Tamalia.*
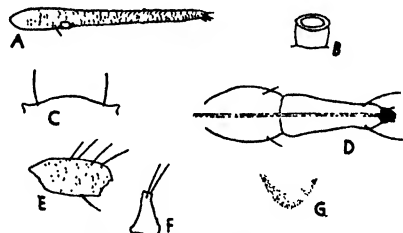
Fig. 10. Genus *Calaphis.*
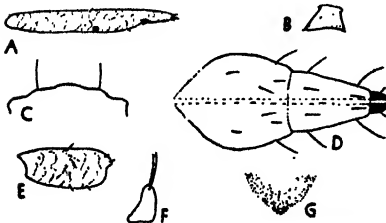
Fig. 11. Genus *Chromaphis.*
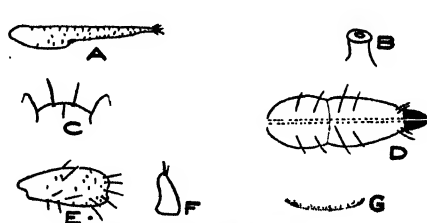
Fig. 12. Genus *Euceraphis.*

thumblike, the spur one-third the length of base. Rostrum broadly obtuse, shorter than body; apical segment small, other segments short and wide and with a few setae. Cornicles short, cylindrical, rimmed. Anal plate triangular, setae not apparent. Dorsal abdominal setation of twelve bristle. First segment of fore tarsus with the two bristles shorter than the inner side; second segment with many setae shorter than the diameter of the segment.

Species examined: *E. californica* (Essig).

Subtribe *Lachnina* Baker 1920

Body large, bearing long hairs. Front rounded. Antennae four-segmented, shorter than body. Dorsal abdominal setation of sixteen or more long hairs. First segment of fore tarsus with two setae.

KEY TO GENERA OF THE LACHNINA

1. Rostrum obtuse ....*Schizolachnus*
   Rostrum acute ....*Lachnus*

Genus **Lachnus** Burmeister 1835
(Fig. 4)

Body large, bearing long hairs. Head wider than long; front rounded, with many long setae. Antennae four-segmented, shorter than body, bearing a few long hairs; spur of terminal segment one-third the length of base. Rostrum acute, longer than body; apical segment long, conelike, bearing many short setae; remaining segments bearing many long setae. Cornicles rims on large, hairy swellings. Anal plate broadly hemispherical, bearing many long setae. Dorsal abdominal setation of eighteen long hairs. First segment of fore tarsus with the two setae shorter than the inner side; second segment bearing many setae longer than the diameter of the segment.

Species examined: *L. curvipes* Patch, *L. edulis* Wilson, *L. glehna* Essig, *L. juniperi* DeGeer, *L. occidentalis* Davidson.

Genus **Schizolachnus** Mordvilko 1908
(Fig. 5)

Body large, elongate, eurypteridiform, bearing conspicuous hairs. Head wider than long; front very slightly rounded, with two setae. Antennae four-segmented, shorter than body, bearing few hairs; spur of terminal segment as long as base. Rostrum obtuse, comparatively parallel-sided, reaching to cornicles; apical segment large and triangular, with a few bristles; remaining segments with a few moderately long setae. Cornicles mere rings. Anal plate triangular, bearing four setae. Dorsal abdominal setation of fourteen long hairs. Abdominal tubercles present. First segment of fore tarsus with the two setae one half the length of the inner side; second segment with a few long setae.

Species examined: *S. pini-radiatae* (Davidson).

Subtribe *Pterochlorina* Oestlund 1918

Only one genus of this subtribe occurs in California, *Pterochlorus*, the characters of which are indicated below.

Genus **Pterochlorus** Rondani 1848

(Fig. 6)

Body large and stout, bearing many long hairs. Head as long as wide; front rounded, with six long setae. Antennae five-segmented, shorter than body, bearing a few hairs; spur of terminal segment as long as base. Rostrum obtuse, at least as long as body; apical segment small, conelike, with a few bristles; remaining segments with many short setae. Cornicles rings on slight hairy swellings. Anal plate hemispherical, bearing many long seta. Dorsal abdominal setation of sixteen long hairs. Abdominal tubercles present. First segment of fore tarsus bearing twelve setae shorter than the inner side; second segment with many short setae.

Species examined: *P. rosae* (Cholodkovsky).

Tribe CALLIPTERINI Oestlund 1887

Front of head rounded, occasionally with frontal tubercles. Antennae usually four-segmented, rarely five-segmented. Rostrum obtuse, usually not longer than body. Cornicles varying from pores to long cylinders. Anal plate rounded or triangular. Dorsal abdominal setation varying from short simple to long capitate hairs. First segment of fore tarsus with the two setae rarely longer than the inner side of the segment; second segment with a few setae longer than the diameter of the segment.

KEY TO SUBTRIBES OF THE CALLIPTERINI

1. Spur of terminal antennal segment shorter than one-half base............Phyllaphidina
   Spur of terminal antennal segment longer than one-half base........................2
2. Cornicles wide rims on swollen bases................................Chaitophorina
   Cornicles not on swollen bases..3
3. Rostrum acute ....Microsiphina
   Rostrum obtuse 4
4. Cornicles approximately as long as wide or porelike......................Callipterina
   Cornicles much longer than wide...5
5. Hairs on antennae not longer than diameter of segments bearing them...Drepanosiphina
   Hairs on antennae nearly twice as long as diameter of segments bearing them.........
                                                                        Pterocommina

Subtribe *Phyllaphidina* Baker 1920

Front of head rounded, frontal tubercles absent. Antennae four-segmented, shorter than body; spur of terminal segment shorter than one-half base. Rostrum obtuse. Cornicles rings or pores. Anal plate broadly rounded. Dorsal abdominal setation varying from bristles to long hairs.

KEY TO GENERA OF THE PHYLLAPHIDINA

1. Rostrum broadly obtuse...*Phyllaphis*
   Rostrum narrowly obtuse...2
2. Cornicles without rims, base of fourth antennal segment long and straight...........
                                                                        Stegophylla
   Cornicles with rims, base of fourth antennal segment short and thick...........*Tamalia*

Genus **Phyllaphis** Koch 1857

Body elongate and narrow, hairs few and inconspicuous. Head wider than long; front rounded, with two long setae. Antennae four-segmented, shorter than body, bearing a few bristles; terminal segment thumblike, the spur half as long as base. Rostrum broadly obtuse, reaching to third pair of coxae; apical segment small, without bristles, remaining segments with a few setae. Cornicles rims on slight swellings. Anal plate hemispherical, bearing four setae. Dorsal abdominal setation apparently of the pleural setae only. First segment of fore tarsus with the two setae half the length of the inner side; second segment with a few short setae.

Species examined: *P. fagi* (Linnaeus).

Genus **Stegophylla** Oestlund 1922
(Fig. 8)

Body elongate and narrow, hairs inconspicuous. Head longer than wide; front rounded, with two short setae. Antennae four-segmented, shorter than body, bearing a few short hairs; spur of terminal segment one-quarter the length of base. Rostrum narrowly obtuse, reaching to third pair of caxae; apical segment small, without bristles, remaining segments with a few long setae. Cornicles rimless openings on slight swellings. Anal plate broadly rounded, bearing four setae. Dorsal abdominal setation apparently consisting of four bristles. First segment of fore tarsus with the two setae not quite so long as the inner side; second segment with a few bristles.

Species examined: *S. quercicola* (Baker).

Genus **Tamalia** Baker 1920
(Fig. 9)

Body ovate, hairs inconspicuous. Head as long as wide; front rounded, with four long setae. Antennae four-segmented, shorter than body, bearing a few hairs; spur of terminal segment one-third the length of base. Rostrum narrowly obtuse, reaching to third pair of coxae; apical segment small, without bristles, remaining segments with many short setae. Cornicles on low conical bases. Anal plate broadly rounded, bearing four setae. Dorsal abdominal setation consisting of six moderately long hairs, with six to eight shorter ones, one to two to the row, in between the longer hairs. First segment of fore tarsus with the two setae as long as the inner side; second segment with a few moderately long setae.

Species examined: *T. coweni* (Cockerell).

Subtribe *Callipterina* Mordvilko 1908

Front of head rounded; frontal tubercles absent or faintly developed. Antennae typically four-segmented and longer than body, occasionally five-segmented or shorter than body; hairs usually less in length than the diameter of the segments bearing them. Rostrum narrowly obtuse. Cornicles short, approximately as long as wide, often rimless. Anal plate triangular or broadly rounded. Dorsal abdominal setation varying from short simple to long simple or capitate hairs.

Genus **Calaphis** Walsh 1863
(Fig. 10)

Body elongate, comparatively parallel-sided, hairs conspicuous. Head wider than long; front slightly rounded, frontal tubercles slightly developed, each with one long simple seta. Antennae four-segmented, longer than body, bearing a few conspicuous hairs; spur of terminal segment twice as long as base. Rostrum narrowly obtuse, reaching just beyond third pair of coxae; apical segment small, with a few bristles; remaining segments with a few short setae. Cornicles short, as long as wide, slightly rimmed. Anal plate triangular, setae apparently absent. Dorsal abdominal setation of six long simple or capitate hairs. First segment of fore tarsus with the two setae as long as the inner side; second segment with a few short setae.

Species examined: *C. betulaecolens* (Fitch), *C. annulata* (Koch).

Genus **Chromaphis** Walker 1870
(Fig. 11)

Body large, ovate, bearing conspicuous capitate hairs. Head as long as wide; front rounded, faintly divided, with two to four long capitate setae, frontal tubercles absent. Antennae three-segmented, reaching about to bases of third pair of coxae, and bearing a few short capitate hairs; terminal segment long, area between apical primary sensorium and proximal primary sensorium slightly longer than spur. Rostrum broadly obtuse, reaching to bases of third pair of coxae; apical segment indistinct, without bristles, remaining segments with a few short setae. Cornicles short, truncate, slightly rimmed. Anal plate roundly triangular, with the tip narrowed and prolonged. Dorsal abdominal setation with the pleural hairs long and capitate and the two dorsal rows very short and bristlelike. First segment of fore tarsus with the two bristles longer than the inner side; second segment with a few setae nearly as long as the diameter of the segment.

Species examined: *C. juglandicola* (Kaltenbach).

Genus **Euceraphis** Walker 1870
(Fig. 12)

Body elongate and thin, comparatively parallel-sided, hairs not conspicuous. Head longer than wide; front rounded, with two long setae, frontal tubercles well developed. Antennae apparently five-segmented, longer than

body, bearing a few short hairs; spur of terminal segment slightly longer than base. Rostrum obtuse, reaching to third pair of coxae; apical segment large and without bristles; remaining segments with a few moderately long setae. Cornicles truncate, slightly rimmed. Anal plate slightly rounded, setae apparently absent. Dorsal abdominal setation of eight long simple hairs. First seg-
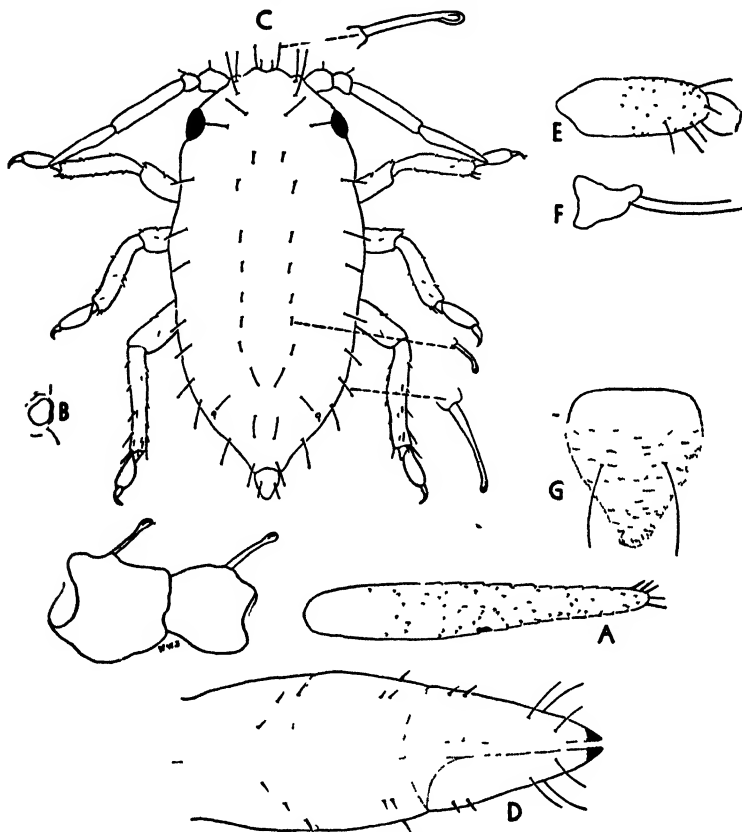
Fig. 13. *Monellia californica* (Essig). First instar nymph.

ment of fore tarsus with the two bristles less than half the length of the inner side; second segment with a moderate number of fairly long setae.

Species examined: *E. betulae* (Koch).

Genus **Monellia** Oestlund 1887
(Figs. 13, 14, 15)

Body of medium size, ovate, bearing conspicuous hairs. Head wider than long; front rounded, faintly divided, bearing two long capitate setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing a few bristles; spur of terminal segment slightly longer than base. Rostrum narrowly obtuse, not quite reaching bases of third pair of coxae; apical segment very small, without bristles; remaining segments with a few setae. Cornicles porelike openings. Anal plate roundly triangular, with the tip prolonged,

bearing two plain setae. Dorsal abdominal setation with the pleural hairs long and capitate, the two dorsal rows short and simple or long and capitate. First segment of fore tarsus with the two setae longer than the inner side; second segment with a few short setae.

Species examined: *M. californica* (Essig), *M. costalis* (Fitch), *M. nigro-punctata* Granovsky.
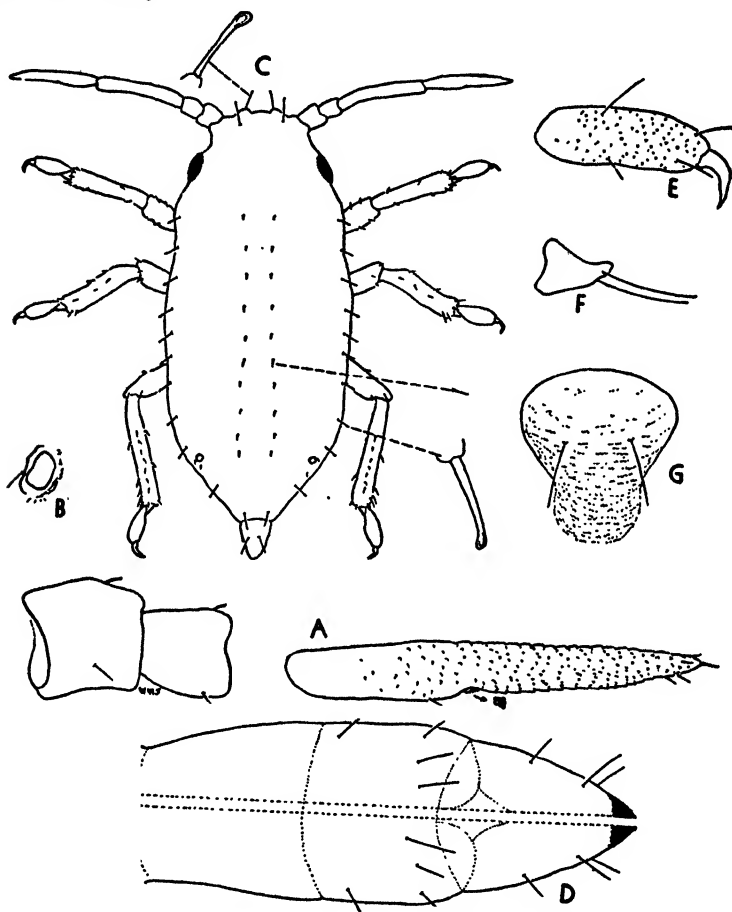
Fig. 14. *Monellia costalis* (Fitch). First instar nymph.

Genus **Myzocallis** Passerini 1860
(Fig. 16)

Body large, ovate, bearing many long hairs, mostly capitate. Head wider than long; front slightly rounded, with two long capitate setae, frontal tubercles very small. Antennae four-segmented, shorter than body, bearing a few hairs shorter than the diameter of the segments bearing them; spur of terminal segment twice as long as base. Rostrum narrowly obtuse, reaching just beyond third pair of coxae; apical segment large, without bristles; remaining segments bearing a few setae of moderate length. Cornicles short, as long as wide, slightly rimmed. Anal plate broadly triangular, bearing two setae. Dorsal

abdominal setation of four long capitate hairs (some specimens seem to have six). First segment of fore tarsus with the two plain setae longer than the inner side; second segment with a few short setae.

Species examined: *M. arundinariae* Essig, *M. coryli* (Goeze), *M. robinae* (Gillette).

Genus **Symydobius** Mordvilko 1894
(Fig. 17)

Body large, ovate, hairs inconspicuous. Head as long as wide; front slightly rounded, with two setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing inconspicuous hairs, third segment longer than all other segments combined; spur of terminal segment as long as base. Rostrum narrowly obtuse, reaching beyond third pair of coxae; apical segment small, without bristles; remaining segments with a few short setae. Cornicles short, slightly longer than wide, rimmed. Anal plate hemispherical, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae slightly less long than the inner side; second segment bearing a few setae slightly longer than the diameter of the segment.

Species examined: *S. agrifoliae* Essig.

Subtribe *Drepanosiphina* Oestlund 1918

Front of head rounded; frontal tubercles present. Antennae five-segmented, of variable length, bearing a few hairs not longer than the diameter of the segments bearing them. Rostrum obtuse. Cornicles much longer than wide. Anal plate rounded. Dorsal abdominal setation variable. First segment of fore tarsus with the two setae shorter in length than the inner side.

KEY TO GENERA OF THE DREPANOSIPHINA

1. Dorsal abdominal setation consisting of long pleural capitate hairs only....*Drepanaphis*
   Dorsal abdominal setation consisting of six bristles...................*Drepanosiphum*

Genus **Drepanaphis** del Guercio 1909
(Fig. 18)

Body large, ovate, bearing conspicuous, capitate hairs. Head wider than long; front slightly rounded, with two to four long capitate setae, frontal tubercles slightly exceeding vertex. Antennae five-segmented, more than twice the length of body, bearing few hairs or bristles; spur of terminal segment fifteen times length of base. Rostrum obtuse, reaching to second pair of coxae; apical segment small, without bristles; remaining segments bearing a few long setae. Cornicles long and cylindrical, bases wider than tips, slightly rimmed. Anal plate broadly rounded, bearing two long simple setae. Last ventral abdominal tergite lobed on each side, each lobe bearing two long, capitate setae. Dorsal abdominal setation apparently consisting only of the long capitate pleural hairs. First segment of fore tarsus with the setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *D. acerfolii* (Thomas).
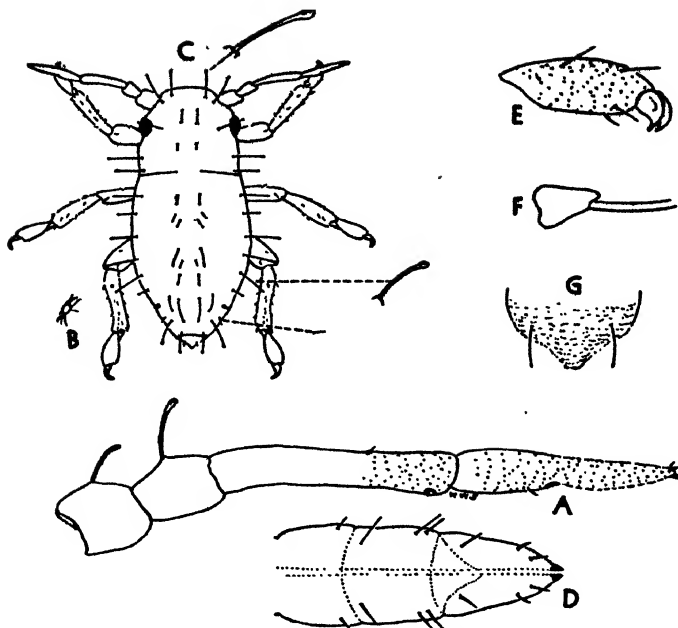
Fig. 15. *Monellia nigropunctata* Granovsky. First instar nymph.
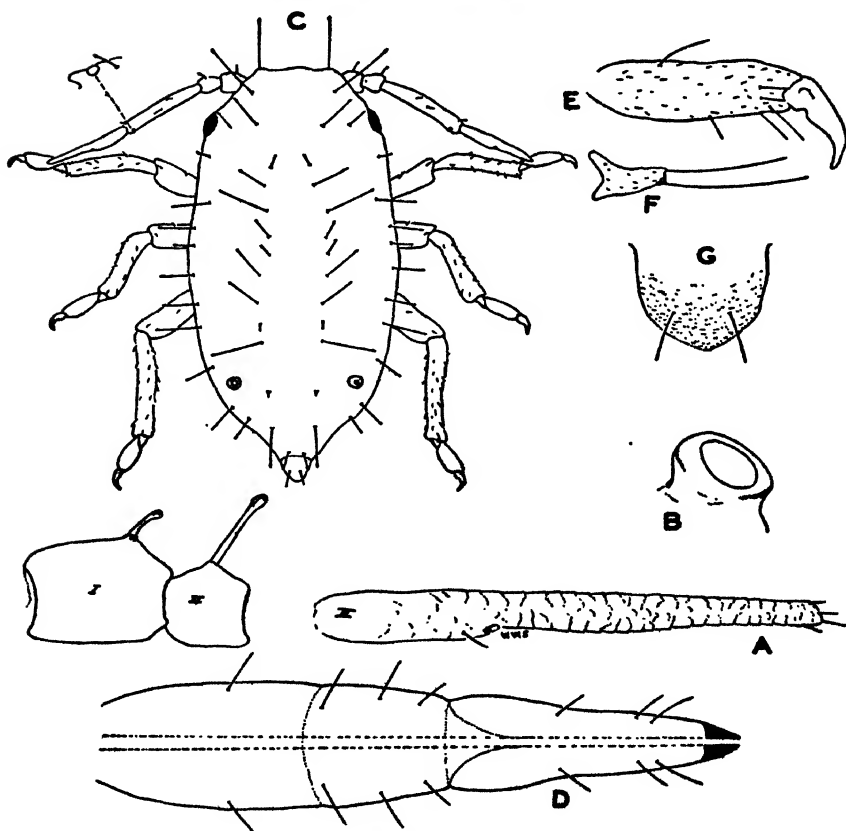
Fig. 16. *Myzocallis coryli* (Goeze). First instar nymph.

Genus **Drepanosiphum** Koch 1855
(Fig. 19)

Body moderate in size, elliptical in shape, hairs not conspicuous. Head wider than long; front rounded, bearing two long setae, frontal tubercles greatly exceeding vertex. Antennae five-segmented, reaching to bases of cornicles, bearing a few bristles; spur of terminal segment four times the length of base. Rostrum obtuse, reaching to third pair of coxae; apical segment small, without bristles; remaining segments with a few short setae. Cornicles long, clavate, imbricated, heavily rimmed. Anal plate hemispherical, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae slightly less long than the inner side; second segment with a few short setae.

Species examined: *D. platanoides* (Schrank).

Subtribe *Chaitophorina* Wilson 1910

Body wide, bearing many long hairs. Head with front slightly rounded; frontal tubercles absent or faintly developed. Antennae four-segmented, shorter than body, bearing many hairs longer than the diameter of the segments bearing them. Rostrum obtuse, shorter than body. Cornicles wide rims on swollen bases. Anal plate rounded. Dorsal abdominal setation consisting of long simple hairs.

KEY TO GENERA OF THE CHAITOPHORINA

1. Dorsal abdominal setation of six hairs.................................*Chaitophorus*
   Dorsal abdominal setation of four hairs.................................*Periphyllus*

Genus **Chaitophorus** Koch 1854
(Fig. 20)

Body wide, bearing conspicuous hairs. Head wider than long; front slightly rounded, with two long setae. Antennae four-segmented, shorter than body, bearing a few hairs longer than the diameter of the segments bearing them; spur of terminal segment about four times the length of base. Rostrum narrowly obtuse, reaching past third pair of coxae; apical segment small, without bristles; remaining segments with a few long setae. Cornicles wide rims on swollen bases. Anal plate subcircular, bearing four long bristles. Dorsal abdominal setation of six long simple hairs. First segment of fore tarsus with the two bristles nearly as long as the inner side; second segment with a few short setae.

Species examined: *C. populifolii* (Essig), *C. populifoliae* Oestlund.

Börner (1930, p. 126) based his genus *Chaitophorinus* on the presence of pleural bristles from the second thoracic to the sixth abdominal tergite. The setation in the thoracic area is a character of specific value only; pleural hairs exist along the sides to the cornicles. This condition exists in the genus *Chaitophorus*. The genus *Chaitophorinus* thus appears to be a synonym of the genus *Chaitophorus*.
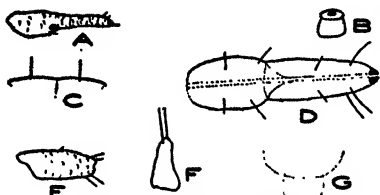
Fig. 17. Genus *Symydobius.*
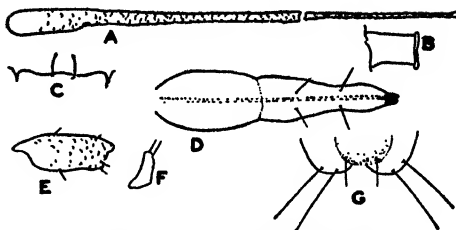
Fig. 18. Genus *Drepanaphis.*
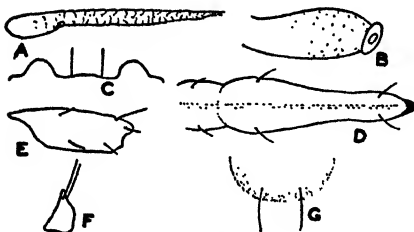
Fig. 19. Genus *Drepanosiphum.*
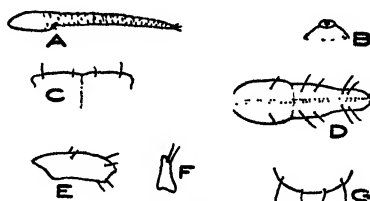
Fig. 20. Genus *Chaitophorus.*
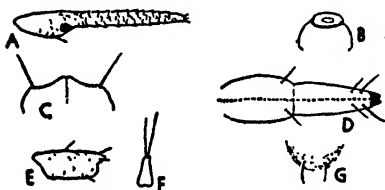
Fig. 21. Genus *Periphyllus.*
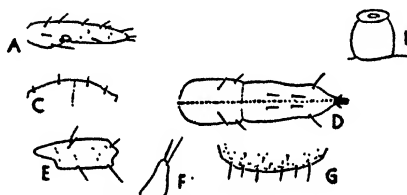
Fig. 22. Genus *Clavigerus.*
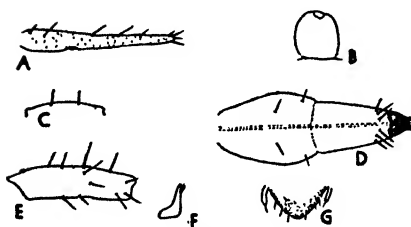
Fig. 23. Genus *Plocamaphis.*
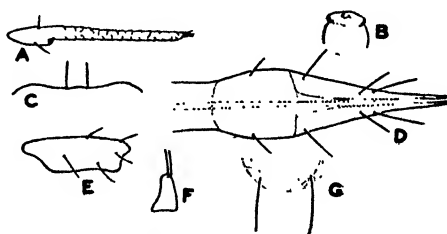
Fig. 24. Genus *Microsiphum.*
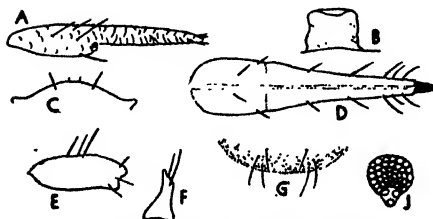
Fig. 25. Genus *Nevadaphis.*
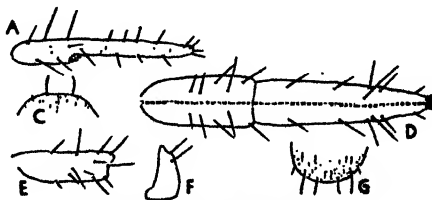
Fig. 26. Genus *Fullawaya.*

Genus **Periphyllus** van der Hoeven 1863
(Fig. 21)

Body ovate, bearing conspicuous hairs. Head longer than wide; front rounded, with two long, simple setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing hairs as long or longer than the diameter of the segments bearing them; spur of terminal segment two to three times longer than base. Rostrum narrowly obtuse, reaching to third pair of coxae; apical segment small, with four bristles; remaining segments with a few short setae. Cornicles wide rings on swollen bases. Anal plate subcircular, bearing two long setae. Last ventral abdominal segment lobed on each side of anal plate, each lobe bearing two long, slightly capitate hairs. Dorsal abdominal setation of four hairs at least as long as the width of the abdomen. First segment of fore tarsus with the two setae twice as long as the inner side; second segment with a few short setae.

Species examined: *P. californiensis* (Shinji), *P. negundinis* (Thomas).

Subtribe *Pterocommina* Wilson 1912

Body large, bearing conspicuous hairs. Front rounded, lacking frontal tubercles. Antennae four-segmented, shorter than body, with hairs about twice as long as the diameter of the segments bearing them. Cornicles elongate and swollen on each side; with or without rims. Anal plate rounded or triangular.

KEY TO GENERA OF THE PTEROCOMMINA

1. Cornicles rimmed...*Clavigerus*
   Cornicles rimless ....*Plocamaphis*

Genus **Clavigerus** Szepligeti 1883
(Fig. 22)

Body large, ovate, bearing many conspicuous hairs. Head wider than long; front rounded, with two long setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing hairs twice as long as the diameter of the segments bearing them; spur of terminal segment at least as long as base. Rostrum obtuse, reaching to bases of cornicles; apical segment small, with four bristles; remaining segments with many long setae. Cornicles long, swollen evenly on each side, with wide, heavy flanges. Anal plates broadly rounded, bearing about eight long setae. Dorsal abdominal setation apparently of eight hairs. First segment of fore tarsus with the two setae at least as long as the inner side; second segment with a few short setae.

Species examined: *C. populifoliae* (Fitch), *C. smithiae* (Monell).

Genus **Plocamaphis** Oestlund 1922
(Fig. 23)

Body large, bearing conspicuous hairs. Head wider than long; front rounded, with two long setae, frontal tubercles absent. Antennae four-segmented, slightly longer than body, bearing many hairs usually longer than the diameter of the segments bearing them; spur of terminal segment twice as long

as base. Rostrum obtuse, longer than body; apical segment very small, with four bristles; remaining segments with a few long setae. Cornioles swollen, bases narrower than tips, rimless. Anal plate broadly triangular, bearing four to six setae. Dorsal abdominal setation of ten long hairs. First segment of fore tarsus with the two setae half the length of the inner side; second segment with a few short setae.

Species examined: *P. flocculosa* (Weed).

Subtribe *Microsiphina* Oestlund 1922

Front of head slightly rounded; frontal tubercles absent. Antennae four- or five-segmented, shorter than body. Rostrum acute. Cornioles as long as wide. Dorsal abdominal setation of six long pointed hairs. First segment of fore tarsus with the two setae not longer than the inner side.

KEY TO GENERA OF THE MICROSIPHINA

1. Ocular tubercles present..*Nevadaphis*
   Ocular tubercles absent..*Microsiphum*

Genus **Microsiphum** Cholodkovski 1908
(Fig. 24)

Body large, ovate, bearing conspicuous simple hairs. Head wider than long; front nearly flat, with two long setae. Antennae five-segmented, reaching to cornioles, bearing a few short hairs; spur of terminal segment three times longer than base. Rostrum acute, reaching past the third pair of coxae; apical segment long and needlelike, without bristles; remaining segments bearing a few conspicuous setae. Cornioles short, not longer than wide, heavily rimmed. Anal plate hemispherical, bearing two long setae. Dorsal abdominal setation of six long pointed hairs. First segment of fore tarsus with the two setae as long as the inner side; second segment with a few setae of medium length.

Species examined: *M. acrophorum* Smith and Knowlton, *Microsiphum* spp.

Genus **Nevadaphis** Drews 1941
(Fig. 25)

Body small, saclike, bearing a few long hairs. Head wider than long; front rounded, with two or four long setae; frontal tubercles absent. Antennae four-segmented, shorter than body, bearing a few long hairs; spur of terminal segment slightly longer than base. Ocular tubercles present, large, taking up one-third of the area of the eyes. Rostrum acute, shorter than body; apical segment small and thin, without bristles; remaining segments with many long setae. Cornioles short, as long as wide, rimless. Anal plate broadly rounded, bearing six long setae. Dorsal abdominal setation of six long pointed hairs. First segment of fore tarsus with the two setae nearly as long as the inner side; second segment with a few setae nearly as long as the diameter of the segment.

Species examined: *N. sampsoni* Drews.

Tribe FULLAWAYINI Baker 1920

There is only one genus in this tribe: *Fullaway*.

Genus **Fullawaya** Essig 1912
(Fig. 26)

Body large, ovate in shape, bearing many long pointed hairs. Head as wide as long; front rounded, with two long setae; frontal tubercles absent. Antennae four-segmented, half as long as body, bearing many hairs longer than the diameter of the segments bearing them; spur of terminal segments twice the length of base. Rostrum narrowly obtuse, longer than body; apical segment very small, with a few bristles; remaining segments with many long setae. Cornicles absent. Anal plate rounded, bearing many long setae. Dorsal abdominal setation of approximately twenty-four long hairs, the exact number not discernible. First segment of fore tarsus with the two setae half the length of the inner side; second segment bearing a few setae longer than the diameter of the segment.

Species examined: *F. saliciradicis* Essig.

Tribe SALTUSAPHIDINI Theobald 1926

Only members of the genus *Thripsaphis* have been available for study.

Genus **Thripsaphis** Gillette 1917
(Fig. 27)

Body elongate, parallel-sided, setose, bearing inconspicuous hairs. Head wider than long; vertex strongly produced and trapezoidal in shape, with two setae. Antennae four-segmented, shorter than body, bearing a few bristles; spur of terminal segment as long as base. Rostrum broadly obtuse, reaching to second pair of coxae; apical segment very short, without bristles; remaining segments with a few moderately long setae. Cornicles thick-walled pores. Anal plate hemispherical, overhung by last abdominal segment, bearing two setae. Dorsal abdominal setation of long pleural hairs and two dorsal rows of bristles. First segment of fore tarsus with the two setae slightly longer than the inner side; second segment bearing a few moderately long setae.

Species examined: *T. verrucosa* Gillette.

Tribe APHIDINI Mordvilko 1908

Head with front flat or rounded, frontal tubercles absent, faintly or greatly developed. Antennae usually four-segmented, occasionally five-segmented, bearing hairs mostly shorter than the diameter of the segment bearing them. Cornicles elongate, rarely porelike. Anal plate triangular or rounded. Rostrum obtuse in most species; apical segment very small or indistinct. Dorsal abdominal setation varying from bristles to long hairs.

KEY TO SUBTRIBES OF THE APHIDINI

1. Frontal tubercles usually exceeding vertex; antennal tubercles.often present; cornicles usually long ....*Macrosiphina*

   Frontal tubercules not exceeding vertex; antennal tubercles absent; cornicles usually short ....*Aphidina*
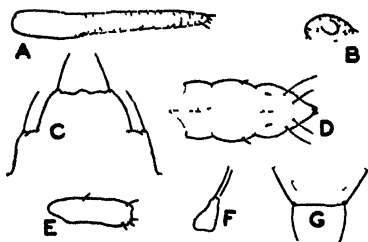
Fig. 27. Genus *Thripsaphis.*
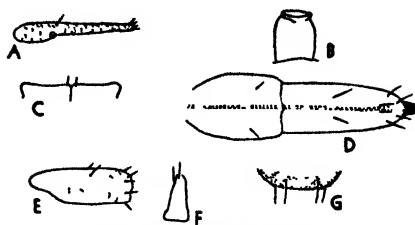
Fig. 28. Genus *Aphis.*
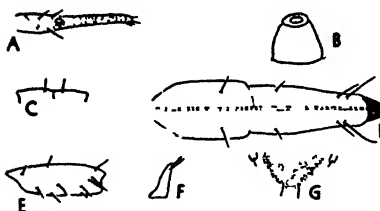
Fig. 29. Genus *Brevicoryne.*
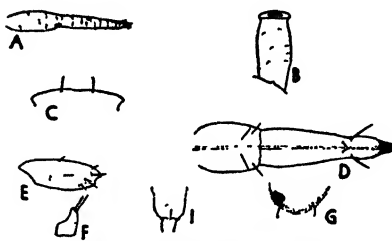
Fig. 30. Genus *Cavariella.*
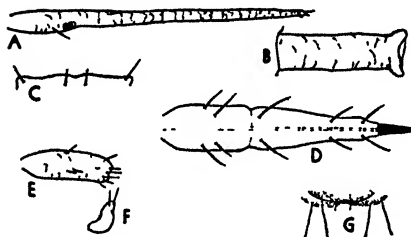
Fig. 31. Genus *Epameibaphis.*
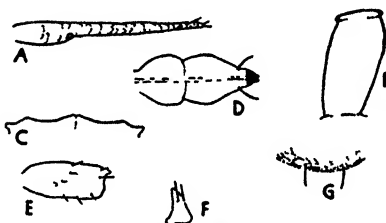
Fig. 32. Genus *Hyalopterus.*
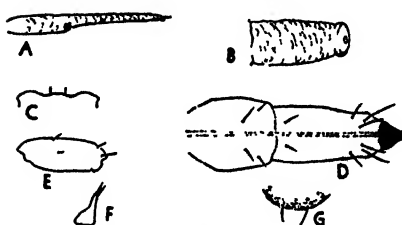
Fig. 33. Genus *Neomyzaphis.*
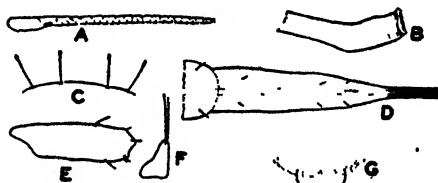
Fig. 34. Genus *Pseudoepameibaphis.*
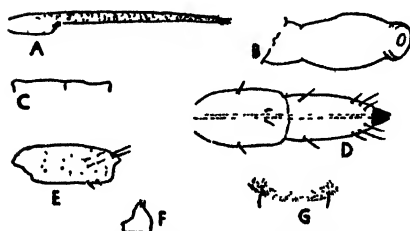
Fig. 35. Genus *Rhopalosiphum.*

Fig. 36. Genus *Siphonatrophia.*

Subtribe *Aphidina* Oestlund 1918

Body small, variable in shape, bearing hairs few and short in most cases. Head with front flat or rounded; frontal tubercles absent or faintly developed. Antennae four- or five-segmented, generally shorter than body, bearing a few hairs usually shorter than the diameter of the segments bearing them. Rostrum in most species obtuse and shorter than body. Cornicles porelike or elongate. Anal plate rounded or triangular. Dorsal abdominal setation of short hairs or bristles, occasionally long hairs.

Genus **Aphis** Linnaeus 1758
(Fig. 28)

Body small, comparatively parallel-sided, hairs inconspicuous. Head as long as wide; front nearly flat, very slightly indented, with two setae, frontal tubercles very faintly indicated. Antenna four-segmented, shorter than body, bearing a few short hairs; spur of terminal segment twice as long as base. Rostrum narrowly obtuse, reaching third pair of coxae; apical segment very small, with or without a few bristles; remaining segments with a few short setae. Cornicles short cylinders, slightly rimmed. Anal plate rounded, bearing two to four bristles. Dorsal abdominal setation of four bristles. Lateral tubercles present. First segment of fore tarsus with the two setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *A. bakeri* Cowen, *A. cardui* Linnaeus, *A. ceanothi* Clarke, *A. cornifoliae* Fitch, *A. gossypii* Glover, *A. helianthi* Monell, *A. helichrysi* Kaltenbach, *A. lutescens* Monell, *A. maidis* Fitch, *A. medicaginis* Koch, *A. persicae-niger* Smith, *A. pomi* DeGeer, *A. rumicis* Linnaeus, *A. sambuci* Lin-

naeus, *A. sambucifoliae* Fitch, *A. sedi* Kaltenbach, *A. tulipae* Boyer de Fonscolombe.

Aphis persicae-niger Smith, and several related species, has been included in the genus *Anuraphis* del Guercio; the first instar nymphs of this group of aphids closely resemble those of *Aphis sambuci* Linnaeus, the type species of the genus *Aphis*. The genus *Anuraphis* del Guercio is a synonym of the genus *Aphis* Linnaeus.

Aphis helichrysi Kaltenbach was made the type species of the genus *Brachycauda* by van der Goot (1913). This species, as seen in the first instar, presents no variation placing it outside the genus *Aphis*.

Börner (1930, p. 162) made *Aphis rumicis* Linnaeus the type species of Risso's genus *Doralis*. This species is a typical member of the genus *Aphis*, and the generic name *Doralis* (Risso) Börner is here made a synonym of *Aphis* Linnaeus.

Aphis bicolor Koch, although not occurring in California, was also examined. This species was made the type of the genus *Hyadaphis* Börner (1930, p. 136); it seems to be a typical member of the genus *Aphis*. The name *Hyadaphis* Börner is preoccupied by *Hyadaphis* Kirkaldy (1904).

Genus **Brevicoryne** van der Goot 1915
(Fig. 29)

Body small, ovate, hairs inconspicuous. Head slightly wider than long; front slightly rounded, with two setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing a few short hairs; spur of terminal segment slightly longer than base. Rostrum narrowly obtuse, reaching past third pair of coxae; apical segment very small, without bristles; remaining segments with a few short setae. Cornicles truncate, with wide rims. Anal plate broadly triangular, bearing two moderately long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae less in length than the inner side; second segment with many setae.

Species examined: *B. brassicae* (Linnaeus), *B. symphoricarpi* (Thomas).

Brevicoryne symphoricarpi (Thomas) differs considerably from the type of the genus, *B. brassicae* (L.); there are differences in the shape of the cornicles and anal plate, and in the length and number of antennal segments. It may well be that the genus *Thargelia*[1] erected for it by Oestlund (1922), is valid, although it is usually placed as a synonym of the genus *Brevicoryne*.

Genus **Cavariella** del Guercio 1911
(Fig. 30)

Body small, ovate, hairs inconspicuous. Head wider than long; front rounded, with two short setae, frontal tubercles absent. Antennae four-segmented, half as long as body, bearing a few short hairs; spur of terminal segment slightly longer than base. Rostrum obtuse, reaching to bases of cornicles; apical segment small, without bristles, remaining segments with a few short setae. Cornicles moderately long, swollen, rimmed. Terminal abdominal

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[1] *Thargelia* Karsh. 1880 used in Arachnida has precedence over *Thargelia* Oestlund 1923.

segment with a dorsal fingerlike projection. Anal plate hemispherical, bearing two short setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae as long as the inner side; second segment with a few short setae.

Species examined: *C. caprae* (Fabricius), *C. pustula* Essig.

Genus **Epameibaphis** Oestlund 1922
(Fig. 31)

Body short and squat, hair conspicuous. Head wider than long; front slightly rounded, with two long, slightly capitate setae, frontal tubercles absent. Antennae four-segmented, longer than body, bearing a few hairs nearly as long as the diameter of the segments bearing them; spur of terminal segment five times longer than base. Rostrum acute, reaching past bases of cornicles; apical segment long and thin, without bristles; remaining segments with long setae. Cornicles long, with knoblike flanges. Anal plate broadly rounded, bearing two setae. Dorsal abdominal setation of twelve long, slightly capitate hairs. First segment of fore tarsus with the two setae nearly as long as the inner side; second segment with a few moderately long setae.

Species examined: *E. utahensis* Knowlton.

Genus **Hyalopterus** Koch 1857
(Fig. 32)

Body elongate, comparatively parallel-sided, hairs inconspicuous. Head longer than wide; front nearly flat, with two setae, frontal tubercles absent. Antennae four-segmented, reaching to bases of cornicles, bearing a few bristles; spur of terminal segment four times the length of base. Rostrum broadly obtuse, reaching to third pair of coxae; apical segment indistinct, without bristles; remaining segments with a few short setae. Cornicles short, swollen, rims barely indicated. Anal plate broadly rounded, with two long setae. Dorsal abdominal setation of four short setae. First segment of fore tarus with the two setae half as long as the inner side; second segment bearing a few short setae.

Species examined: *H. arundinis* (Fabricius).

Genus **Myzaphis** van der Goot 1913
(Figs. 1 and 2)

Body of moderate size, elongate-ovate, hairs inconspicuous. Head as long as wide; front rounded, vertex produced, with two long setae, frontal tubercles absent. Antennae four-segmented, not reaching third pair of coxae, bearing a few bristles; spur of terminal segment slightly longer than base. Rostrum broadly obtuse, shorter than body; apical segment small, without bristles; remaining segments with many short setae. Cornicles long, smooth, constricted before tips, heavily rimmed. Anal plate roundly triangular, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae nearly as long as the inner side; second segment with a few short setae.

Species examined: *M. rosarum* (Kaltenbach).

Genus **Neomyzaphis** Theobald 1926
(Fig. 33)

Body small, ovate, hairs inconspicuous. Head wider than long; front rounded, vertex slightly produced, with two short setae, frontal tubercles present, not exceeding vertex. Antennae four-segmented, reaching to bases of cornicles, bearing a few hairs shorter than the diameter of the segments bearing them; spur of terminal segment twice as long as base. Rostrum narrowly obtuse, as long as body; apical segment small, with a few bristles; remaining segments with a few short setae. Cornicles long, heavily imbricated and rimmed. Anal plate rounded, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *N. abetina* (Walker).

Genus **Pseudoepameibaphis** Gillette and Palmer 1932
(Fig. 34)

Body large, ovate, with conspicuous fan-shaped hairs. Head wider than long; front slightly rounded, with four long capitate setae, frontal tubercles absent. Antennae five-segmented, reaching to third pair of coxae, bearing a few setae; spur of terminal segment five times length of base. Rostrum acute, reaching to third pair of coxae; apical segment long and thin, without bristles, remaining segments with many short setae. Cornicles long, crooked in upper quarter, heavily rimmed. Anal plate hemispherical, with two simple setae. Dorsal abdominal setation of eight long, fan-shaped hairs. First segment of fore tarsus with the two setae slightly longer than the inner side; second segment with a few short setae.

Species examined: *P. glauca* Gillette and Palmer.

Genus **Rhopalosiphum** Koch 1854
(Fig. 35)

Body small, hairs inconspicuous. Head about as long as wide; front rounded, with two short setae, frontal tubercles very faintly indicated. Antennae four-segmented, shorter than body, bearing a few short hairs; spur of terminal segment five to six times longer than base. Rostrum narrowly obtuse, reaching about to third pair of coxae; apical segment small, without bristles, remaining segments with a few short setae. Cornicles long, swollen, heavily rimmed. Anal plate broadly rounded, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae half the length of the inner side; second segment with a few short setae.

Species examined: *R. berberdis* (Kaltenbach), *R. nymphaeae* (Linnaeus), *R. pseudobrassicae* (Davis), *R. conii* (Davidson), *R. prunifoliae* (Fitch).

Genus **Siphonatrophia** Swain 1918
(Fig. 36)

Body small, ovate, hairs very inconspicuous. Head wider than long; front rounded, with two small setae, frontal tubercles absent. Antennae four-segmented, shorter than body, bearing a few bristles; spur of terminal segment

slightly longer than base. Rostrum obtuse, reaching to third pair of coxae; apical segment indistinct, without bristles; remaining segments with a few short setae. Cornicles porelike. Anal plate broadly triangular, bearing two setae. Dorsal abdominal setation not evident. First segment of fore tarsus with the two setae very short; second segment with a few short setae.

Species examined: *S. cupressi* (Swain).

Genus **Toxoptera** Koch 1857
(Fig. 37)

Body small, ovate, hairs inconspicuous. Head wider than long; front rounded, with two long setae, frontal tubercles faintly developed. Antennae four-segmented, shorter than body, bearing a few short hairs; spur of terminal segment five times longer than base. Rostrum narrowly obtuse, reaching past the third pair of coxae; apical segment indistinct, without bristles; remaining segments with a few moderately long setae. Cornicles short, imbricated, slightly rimmed, the upper portion slightly swollen. Anal plate hemispherical, bearing two setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus half the length of the inner side; second segment with a few short setae.

Species examined: *T. aurantii* (B. de Fonsc.).

Genus **Yezabura** Matsumûra 1917
(Fig. 38)

Body small, elongate-ovate, hairs conspicuous. Head trapezoidal, about as long as wide; front nearly flat, with four long setae, frontal tubercles slightly developed. Antennae four-segmented, shorter than body, bearing a few hairs as long as the diameter of the segments bearing them; spur of terminal segment three times the length of base. Rostrum obtuse, reaching to bases of third pair of coxae; apical segment indistinct, without bristles; remaining segments with a few long setae. Cornicles short, swollen, slightly rimmed. Anal plate hemispherical, bearing two long setae. Dorsal abdominal setation of six moderately long hairs. First segment of fore tarsus with the two setae very small; second segment with a few moderately long setae.

Species examined: *Y. eriophori* (Walker).

The exact generic position of the above species is uncertain. It has been placed in many genera, among them the genus *Aphis*. Although it falls into the subtribe Aphidina, it does not fall into the genus *Aphis* or any of the genera closely related to it. The species itself has often been placed as a synonym of *Aphis viburnicola* Gillette, but I am following Essig (1939) in holding the species to be distinct from *A. viburnicola* and placing it in the genus *Yezabura*.

Subtribe *Macrosiphina* Oestlund 1918

Head with front flat or rounded, frontal tubercles present, prolonged beyond vertex, antennal tubercles often present. Antennae four-segmented, occasionally five-segmented, usually with hairs less in length than the diameter of the segments bearing them. Cornicles elongate. Anal plate rounded
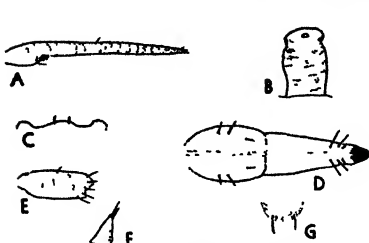
Fig. 37. Genus *Toxoptera.*
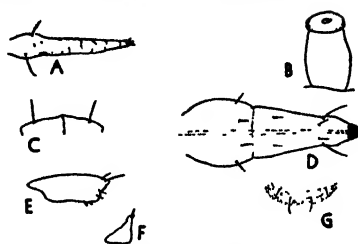
Fig. 38. Genus *Yezabura.*
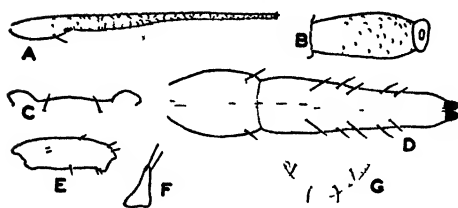
Fig. 39. Genus *Amphorophora.*
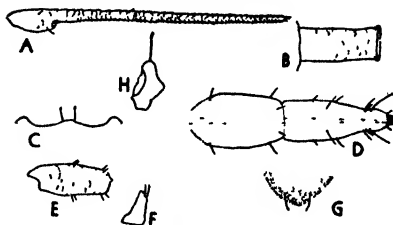
Fig. 40. Genus *Capitophorus.*
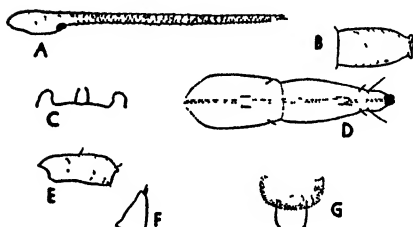
Fig. 41. Genus *Idiopterus.*
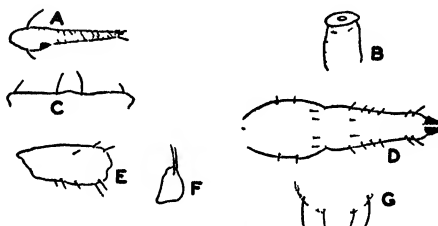
Fig. 42. Genus *Kakimia.*
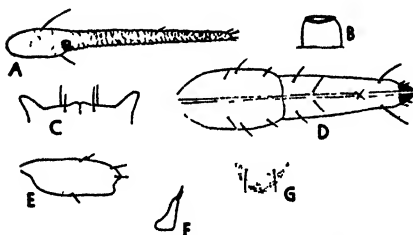
Fig. 43. Genus *Macrosiphoniella.*
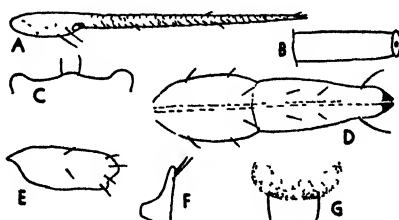
Fig. 44. Genus *Macrosiphum.*
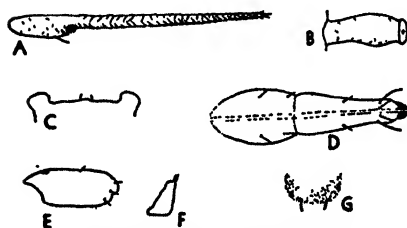
Fig. 45. Genus *Micromyzus.*
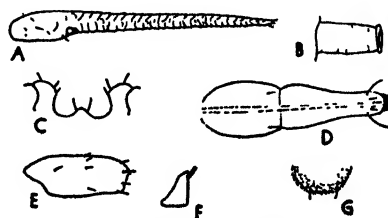
Fig. 46. Genus *Myzus.*

or triangular. Rostrum narrowly obtuse, the apical segment small. Dorsal abdominal setation varying from hairs to bristles, typically six in number.

Genus **Amphorophora** Buckton 1876
(Fig. 39)

Body large, ovate, hairs usually not prominent. Head about as wide as long; front nearly flat, frontal tubercles exceeding vertex. Antennae four- or five-segmented, at least as long as body, bearing a few hairs shorter than the diameter of the segments bearing them; spur of terminal segment three times longer than base. Rostrum narrowly obtuse, reaching past third pair of coxae; apical segment small, with a few bristles; remaining segments with many short or long setae. Cornicles clavate, swollen evenly on both sides. Anal plate hemispherical, bearing two or four long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae half the length of the inner side; second segment with a few short setae.

Species examined: *A. morrisoni* (Swain), *A. nervata* (Gillette), *A. rubi* (Kaltenbach), *A. rubicola* (Oestlund), *A. sonchi* (Oestlund).

Genus **Capitophorus** van der Goot 1913
(Fig. 40)

Body elongate, narrowly ovate to parallel-sided, hairs conspicuous and capitate. Head about as wide as long; front rounded, with two long capitate setae, frontal tubercles exceeding vertex. Antennae four-segmented, reaching past bases of cornicles, bearing a few short hairs; spur of terminal segment five times longer than base; first segment with a process projecting forward, often bearing a capitate hair on its vertex. Rostrum narrowly obtuse, reaching to third pair of coxae; apical segment small, with two bristles; remaining seg-

ments with a few short setae. Cornicles long and cylindrical, slightly imbricated, rimmed. Anal plate triangular, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae half the length of the inner side; second segment with a few short setae.

Species examined: *C. braggii* (Gillette), *C. potentillae* (Walker), *C. ribis* (Linnaeus), *C. tetrarhodus* (Walker), *C. fragaefolii* (Cockerell).

Genus **Idiopterus** Davis 1900
(Fig. 41)

Body elongate, parallel-sided, hairs inconspicuous. Head wider than long; front slightly rounded, with two long capitate setae, frontal tubercles large and conical, directed forward. Antennae four-segmented, longer than body, bearing a few short setae; spur of terminal segment five times longer than base. Rostrum narrowly obtuse, as long as body; apical segment very small, without bristles; remaining segments with a few short setae. Cornicles moderately long, imbricated, bases wider than tips. Anal plate subcircular, bearing two long capitate setae. Dorsal abdominal setation of six short capitate hairs. First segment of fore tarsus with the two setae much shorter than the inner side; second segment with a few short setae.

Species examined: *I. nephrelepidis* Davis.

Genus **Kakimia** Hottes and Frison 1931
(Fig. 42)

Body small, narrowly ovate, hairs conspicuous, simple to slightly capitate. Head wider than long; front nearly flat, with two long setae, frontal tubercles slightly exceeding vertex. Antennae four-segmented, shorter than body, bearing a few hairs nearly as long as the diameter of the segments bearing them; spur of terminal segment three times longer than base. Rostrum narrowly obtuse, reaching past third pair of coxae; apical segment large, without bristles; remaining segments with numerous long setae. Cornicles moderately long, cylindrical, rimmed. Anal plate broadly rounded, bearing four setae. Dorsal abdominal setation of twelve hairs. First segment of fore tarsus with the two setae about as long as the inner side; second segment with a few long setae.

Species examined: *K. castellieae* Sampson, *K. mimulicola* Drews and Sampson, *K. ribifolii* (Davidson).

Genus **Macrosiphoniella** del Guercio 1911
(Fig. 43)

Body elongate and narrow, hairs conspicuous. Head as long as wide; front slightly rounded, with two long setae, frontal tubercles prominent and diverging. Antennae four-segmented, longer than body, bearing hairs less in length than the diameter of the segments bearing them; spur of terminal segment four times longer than base. Rostrum narrowly obtuse, reaching to end of abdomen; apical segment small, with four bristles; remaining segments with many short setae. Cornicles cylindrical, twice as long as wide, slightly rimmed.

Anal plate broadly triangular, bearing two long setae. Dorsal abdominal seta-tion of six long hairs. First segment of fore tarsus with the two setae one-third the length of the inner side; second segment with a few short setae.

Species examined: *M. sanborni* (Gillette).

Genus **Macrosiphum** Passerini 1860
(Fig. 44)

Body large, hairs inconspicuous to conspicuous, simple to capitate. Head usually about as long as wide; front slightly rounded, with two long setae, frontal tubercles exceeding vertex, antennal tubercles often present. Antennae four- or five-segmented, reaching beyond the third pair of coxae, bearing a few short to long hairs; spur of terminal segment five times longer than base. Rostrum usually narrowly obtuse, sometimes acute; reaching beyond third pair of coxae; setation variable. Cornicles long, usually cylindrical, occasionally slightly swollen on one side. Anal plate broadly rounded, bearing two long setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae half the length of the inner side; second segment with few to many short setae.

Species examined: *M. albifrons* Essig, *M. ambrosiae* (Thomas), *M. frigidae* (Oestlund), *M. californicum* (Clarke), *M. pisi* (Kaltenbach), *M. rudbeckiae* (Fitch), *M. rosae* (Linnaeus), *M. solanifolii* (Ashmead).

Genus **Micromyzus** van der Goot 1916
(Fig. 45)

Body moderately sized, narrowly ovate, hairs inconspicuous. Head as long as wide; front nearly flat, with two short setae, frontal tubercles exceeding vertex, converging. Antennae four-segmented, longer than body, bearing a few short hairs; spur of terminal segment five times longer than base. Rostrum narrowly obtuse, reaching beyond third pair of coxae; apical segment small, without bristles; remaining segments with a few short setae. Cornicles moder-ately long, faintly swollen in the upper quarter, slightly rimmed. Anal plate hemispherical, bearing two short setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *M. formosana* (Takahashi).

Genus **Pentalonia** Coquerel 1859
(Fig. 46)

Body small, elongate, hairs inconspicuous. Head as long as wide; front rounded, with two short setae, frontal tubercles greatly exceeding vertex, imbricated and converging. Antennae four-segmented, as long as body, bear-ing a few very short hairs; spur of terminal segment about ten times longer than base; first antennal segment projecting slightly inward. Rostrum nar-rowly obtuse, reaching to bases of cornicles; apical segment small, without setae; remaining segments with a few short setae. Cornicles long, imbricated, swollen in the upper portion. Anal plate rounded, bearing two long setae.
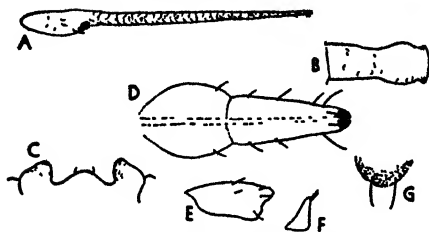
Fig. 47. Genus *Pentalonia*.
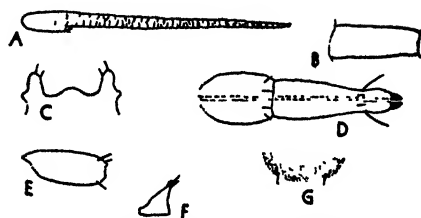
Fig. 48. Genus *Phorodon*.
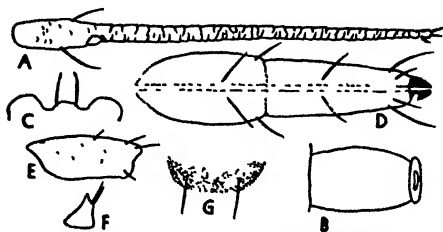
Fig. 49. Genus *Rhopalosiphoninus*.
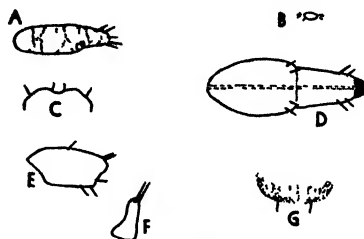
Fig. 50. Genus *Mindarus*.
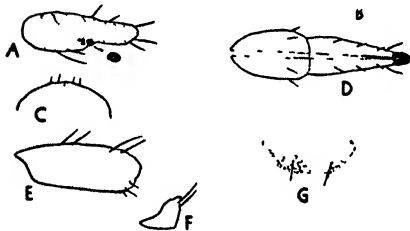
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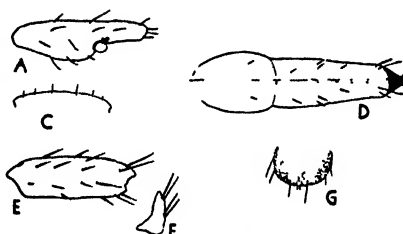
Fig. 52. Genus *Forda*.
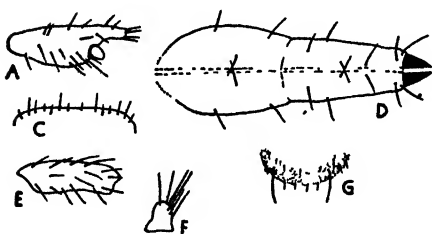
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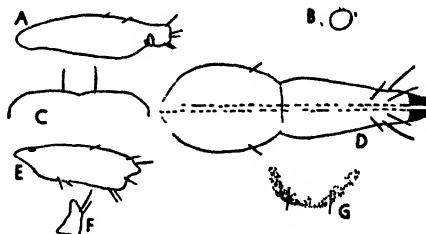
Fig. 54. Genus *Pemphigus*.
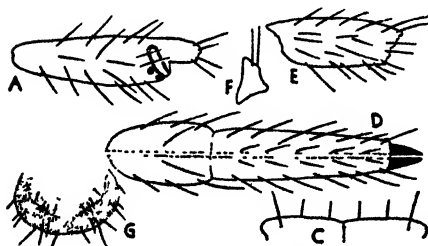
Fig. 55. Genus *Prociphilus*.
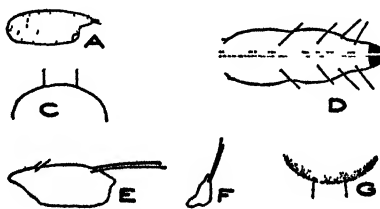
Fig. 56. Genus *Hamamelistes*.

Dorsal abdominal setation of six bristles. First segment of fore tarsus less than half the length of the inner side; second segment with a few short setae.

Species examined: *P. nigronervosa* Coquerel.

Genus **Myzus** Passerini 1860
(Fig. 47)

Body moderately sized, hairs inconspicuous. Head wider than long; front slightly rounded, with two long setae, frontal tubercles large, converging, exceeding vertex. Antennae four- to five-segmented, shorter than body, bearing a few short hairs; spur of terminal segment twice as long as base. Rostrum narrowly obtuse, shorter than body; apical segment small, without bristles; remaining segments with a few short setae. Cornicles short to long, cylindrical, rimmed. Anal plate rounded, bearing two setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *M. cerasi* (Fabricius), *M. circumflexus* (Buckton), *M. convolvuli* (Kaltenbach), *M. ornatus* Laing, *M. persicae* (Sulzer), *M. phloxae* (Sampson).

Genus **Phorodon** Passerini 1860
(Fig. 48)

Body small, ovate, hairs inconspicuous. Head longer than wide; front slightly rounded, with two short setae, frontal tubercles long and fingerlike, directed forward, often with two thick setae. Antennae four-segmented, bearing a few short hairs; spur of terminal segment five times longer than base; first segment with an inwardly projecting process, bearing several thick bristles. Rostrum narrowly obtuse, shorter than body; apical segment small, without bristles; remaining segments with a few short setae. Cornicles of medium length, cylindrical, rimmed. Anal plate broadly rounded, bearing two short setae. Dorsal abdominal setation of six bristles. First segment of fore tarsus with the two setae less than half the length of the inner side; second segment with a few short setae.

Species examined: *P. humuli* (Schrank), *P. menthae* (Buckton).

Genus **Rhopalosiphoninus** Baker 1920
(Fig. 49)

Body large, parallel-sided, bearing a few conspicuous hairs. Head as long as wide; front rounded, with two long, slightly capitate hairs, frontal tubercles broadly rounded, exceeding vertex. Antennae four-segmented, longer than body, bearing a few hairs longer than the diameter of the segments bearing them; spur of terminal segment six times longer than base. Rostrum narrowly obtuse, shorter than body; apical segment large, without bristles; remaining segments with a few long setae. Cornicles long, very wide, swollen toward the center, rims very wide. Dorsal abdominal setation of six moderately long, slightly capitate hairs. First segment of fore tarsus with the two setae nearly as long as the inner side; second segment with a few short setae.

Species examined: *R. latysiphon* (Davidson).

Subfamily MINDARINAE Baker 1920

There is only one genus in this subfamily, *Mindarus,* the characters of which are given below.

Genus **Mindarus** Koch 1857

(Fig. 50)

Body small, ovate, hairs inconspicuous. Head as long as wide, somewhat trapezoidal in shape; front flattened, indented and divided, with four short setae; frontal tubercles absent. Eyes three-faceted. Antennae five-segmented, shorter than body, bearing a few bristles; spur of terminal segment one-quarter the length of the base, the primary sensorium oval. Rostrum obtuse, longer than body; apical segment very small, without bristles; remaining segments setulose and with a few short setae. Cornicles mere pores. Anal plate rounded, bearing two short setae. Dorsal abdominal setation of six bristles. Abdominal tubercles present. First segment of fore tarsus with the two setae nearly as long as the inner side; second segment with a few short setae.

Species examined: *M. abietinus* Koch.

Subfamily PEMPHIGINAE Passerini 1863

Head wider than long; frontal tubercles absent. Spur of terminal antennal segment shorter than base; primary sensorium on base narrow and transverse, or oval and tuberculate. Eyes three-faceted. Cornicles mere pore or absent. Anal plate rounded. Setae on first segment of fore tarsus long, typically two in number, sometimes more.

KEY TO TRIBES OF THE PEMPHIGINAE

1. Cornicles present 2
   Cornicles absent 3
2. Primary sensorium of terminal antennal segment not ciliate . . . . .Pemphigini
   Primary sensorium of terminal antennal segment ciliate . . . . .Eriosomatini
3. Primary sensorium of terminal antennal segment oval and tuberculate . . . . .Fordini
   Primary sensorium of terminal antennal segment narrow and transverse . . . .Prociphilini

Tribe ERIOSOMATINI Baker 1920

Only members of the genus *Eriosoma* have been available for study.

Genus **Eriosoma** Leach 1818

(Fig. 51)

Body large, ovate, hairs usually inconspicuous. Head wider than long; front rounded, with two to four short setae, frontal tubercles absent. Eyes three-faceted. Antennae four-segmented, shorter than body, bearing few to many hairs not longer than the diameter of the segments bearing them; spur of terminal segment shorter than base, the primary sensorium on base oval and ciliate. Rostrum broadly acute, longer than body; apical segment small without bristles; remaining segments with a few moderately long setae. Cornicles mere pores. Anal plate broadly rounded, bearing two setae. Dorsal abdominal setation of six moderately long hairs. First segment of fore tarsus with the two setae as long as the inner side; second segment with a few short setae.

Species examined: *E. americanum* Riley, *E. lanigerum* (Hausmann), *E. lanuginosum* (Hartig).

Marchal (1933) showed two long capitate hairs on the dorsum of the second tarsal segment of *E. lanuginosum;* such hairs were not found on specimens from California. He also showed the tarsus to be one-segmented; such a condition was not observed in California specimens.

Tribe FORDINI Baker 1920

Head rounded, frontal tubercles absent. Antennae four- or five-segmented, usually bearing conspicuous hairs; primary sensorium of terminal antennal segment oval and tuberculate. Cornicles absent. Anal plate rounded. Rostrum obtuse. Dorsal abdominal setation of long or short hairs. First tarsal segment of fore tarsus with four or more setae.

KEY TO GENERA OF THE FORDINI

1. Dorsal abdominal setation of many long conscipuous hairs.....................*Forda*
   Dorsal abdominal setation of many short inconspicuous hairs..............*Trifidaphis*

Genus **Forda** von Heyden 1837
(Fig. 52)

Body large, ovate, hairs inconspicuous. Head wider than long, somewhat trapezoidal in shape; front slightly rounded, with two or four short setae. Antennae five-segmented, shorter than body, bearing a few short hairs; spur of terminal antennal segment shorter than base, the primary sensorium on base oval and tuberculate. Rostrum obtuse, shorter than body; apical segment very small, with a few bristles; remaining segments with many short setae. Cornicles absent. Anal plate hemispherical, bearing many long setae. Dorsal abdominal setation of about thirty-two short hairs, irregularly arranged. First segment of fore tarsus with four long setae; second segment with many short setae.

Species examined: *F. olivacea* Rohwer.

Genus **Trifidaphis** del Guercio 1909
(Fig. 53)

Body large, saclike, bearing conspicuous hairs. Head wider than long; front nearly flat, with many short setae. Antennae four-segmented, shorter than body, bearing many long hairs; spur of terminal segment one-quarter the length of base, the primary sensorium on base oval and tuberculate. Rostrum narrowly obtuse, slightly longer than body; apical segment large, without bristles; remaining segments with a few long setae. Cornicles absent. Anal plate rounded, bearing two long setae. Dorsal abdominal setation of many long hairs, the exact number not discernible, but more than twenty. First segment of fore tarsus with six or more setae longer than the inner side; second segment with many setae longer than the diameter of the segment.

Species examined: *T. radicicola* (Essig).

Tribe PEMPHIGINI Thomas 1879

Only members of the genus *Pemphigus* have been available for study.

Genus **Pemphigus** Hartig 1837
(Fig. 54)

Body large, elongate-ovate, hairs inconspicuous. Head wider than long; front slightly rounded, with two long setae. Antennae four-segmented, shorter than body, bearing a few short setae; spur of terminal segment very short, the primary sensorium on base narrow and transverse. Rostrum acute, shorter than body; apical segment large, without bristles; remaining segments with a few long setae. Cornicles mere pores. Anal plate rounded, bearing two long setae. Dorsal abdominal setation of six hairs. First segment of fore tarsus with the two setae not as long as the inner side; second segment with a few short setae.

Species examined: *P. populicaulis* (Fitch).

Tribe PROCIPHILINI Oestlund 1918

Only members of the genus *Prociphilus* have been available for study.

Genus **Prociphilus** Koch 1857
(Fig. 55)

Body large, ovate, with conspicuous hairs. Head wider than long; front slightly rounded, with several long setae. Antennae four-segmented, shorter than body, bearing few to many hairs at least as long as the diameter of the segments bearing them; spur of terminal segment one-third the length of base, the primary sensorium on the base narrow and transverse. Rostrum acute, at least as long as body; apical segment large, with a few bristles; remaining segments with many long setae. Cornicles absent. Anal plate hemispherical, bearing many long setae. Dorsal abdominal setation of six long or short hairs. First segment of fore tarsus with the two setae longer than the inner side; second segment with many moderately long setae.

Species examined: *P. fraxini-dipetalae* (Essig), *P. populi-monilis* (Riley), *Prociphilus* spp.

My careful examination of the first instar nymph of *populi-monilis* (Riley), which has been included in the genus *Thecabius* Koch (1857), has failed to reveal any salient differences that warrant putting it in the genus *Thecabius*.

Subfamily HORMAPHIDINAE Börner 1908

Head rounded, without frontal tubercles. Antennae three- to four-segmented, shorter than body; spur of terminal segment much shorter than base. Eyes three-faceted. Cornicles elongate or absent. Anal plate rounded. First segment of fore tarsus with two long setae; second segment with two long, slightly capitate setae on the dorsum.

KEY TO TRIBES OF THE HORMAPHIDINAE

1. Cornicles present . . . . .Cerataphidini
   Cornicles absent. . . . . .Hormaphidini

Tribe HORMAPHIDINI Tullgren 1909

Only members of the genus *Hamamelistes* have been available for study.

Genus Hamamelistes Shimer 1867
(Fig. 56)

Body small, elongate-oval, hairs inconspicuous. Head wider than long; front rounded, with four short setae. Antennae four-segmented, shorter than body, bearing a few very short setae; spur of terminal segment barely indicated, base large and thick, the primary sensorium oval. Rostrum obtuse, reaching to third pair of coxae; apical segment small, without bristles; remaining segments with a few long setae. Cornicles absent. Dorsal abdominal setation of four short hairs. Anal plate broadly rounded, bearing four short setae. First segment of fore tarsus with the two setae much longer than the inner side; second segment with two long, slightly capitate setae, and a few shorter ones.

Species examined: *H. agrifoliae* Ferris, *H. spinosus* Shimer.

Only first instar nymphs of the leaf rolling or fourth generation are described. For nymphs of the other generations, see Pergande (1901).
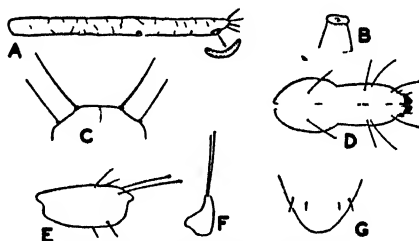
Fig. 57. Genus *Thoracaphis.*

Tribe CERATAPHIDINI van der Goot 1916

Genus Thoracaphis Van der Goot 1917
(Fig. 57)

Body small, elongate, hairs conspicuous. Head wider than long; front rounded, with four very long setae. Antennae three-segmented, half as long as body, bearing a few long hairs; spur of terminal segment one-quarter the length of base, the primary sensorium transverse. Rostrum obtuse, reaching beyond third of coxae; apical segment small, with a few bristles; remaining segments with a few long setae. Cornicles elongate, trumpetlike. Dorsal abdominal setation of four very long hairs. First segment of fore tarsus with the two long, slightly capitate setae much longer than the inner side; second segment with two long, slightly capitate setae on the dorsum and a few short plain ones.

Species examined: *T. umbellulariae* Essig.

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THE INSECT PARASITES
OF THE CHRYSOPIDAE
(NEUROPTERA)

BY

DONALD W. CLANCY

CONTENTS

THE INSECT PARASITES OF THE CHRYSOPIDAE (NEUROPTERA)

BY

DONALD W. CLANCY

INTRODUCTION

ALTHOUGH considerable biological information has been accumulated on the parasites of the Syrphidae and Coccinellidae, the family Chrysopidae, which is similar in habit and in economic significance, has been almost entirely neglected from that standpoint. The only published account on the bionomics of any *Chrysopa* parasite is that of H. S. Smith (1917) on the oviposition habits and primary larva of *Perilampus chrysopae* Cwfd.

Although the majority of records were obtained incidental to other work, and refer only to individual species, several authors have published more extensive lists. Howard (1890) summarized the existing American and European records; McGregor (1914) and McGregor and McDonough (1917) listed species from chrysopids on cotton in South Carolina; R. C. Smith (1922) recorded several parasites from the eastern and southern states, and Cole (1933) in California noted species bred from chrysopids preying upon citrus-infesting mealybugs. In Canada Putman (1937) encountered several parasites while investigating chrysopids as predators of the Oriental fruit moth. Swezey (1936) gives information on species reared in the Hawaiian Islands, and Killington (1936) has summarized most of the European records, including those of Withycombe (1923) in England.

From preliminary sample rearings in southern California, an exceptionally rich and varied parasitic fauna was indicated. Little or no biological information existed on the members of certain of these groups. It was decided therefore to investigate the biology of each species, concentrating upon those which might exhibit new or unusual features; to summarize all published records; and attempt to accumulate information on field parasitism.

ACKNOWLEDGMENTS

LABORATORY AND FIELD TECHNIQUES

Both *Chrysopa californica* Coq. and *C. majuscula* Banks were readily propagated on aphis-infested potato sprouts in the insectary. Tubers were planted in wooden trays and placed in cloth-covered cages where temperatures of 70°

to 80° F., and 60 per cent relative humidity prevailed. Cultures of citrus-infesting mealybugs (*Pseudococcus* spp.), as used in the production of Cryto-laemus (Smith and Armitage, 1931), in combination with aphis were most satisfactory, since the green tips were soon withered by the feeding of large aphis populations; the mealybugs then served as prey. Wads of burlap placed behind the trays and among the sprouts were examined for cocoons and mature larvae to be used in laboratory studies. Oviposition was restricted with mealybugs alone, and in vial rearings the young larvae frequently became entangled in the cottony egg masses. Mature female lacewings were readily attracted to lighted windows at night, and rearing cages were thus kept well supplied. Hundreds of eggs were deposited upon the window screen in a single evening; these were frequently removed for individual rearings.

For laboratory parasitization, host individuals were exposed in glass vials and the cocoons transferred to gelatine capsules secured to sections of cardboard with strips of Scotch drafting tape, the necessary data being recorded alongside. The parasitized material is thus readily handled and may be moved about without danger of breakage or confusion. In order to follow the development of ectoparasitic species, depressed slides were used with cover slip tops; heated metal pinheads pressed into paraffine blocks created smaller cells of various sizes.

Dissections were made in normal salt solution, and the illustrations, all of which are original, were made from living or freshly killed specimens with the aid of a camera lucida. Glycerine or Hoyer's solution gave best results in studying the tracheal systems, whereas larvae pressed in xylol beneath cover slips showed the mandibles to best advantage. In addition, permanent mounts of eggs and larvae were made in Hoyer's solution after staining with acid fuchsin in lactophenol (Maple, 1937).

In order to secure data on field parasitism, cocoons were systematically collected from banded trees in thirteen separate localities in southern California. The bands were doubled loosely about the trunks of walnut, apple, and orange trees. Each cocoon was isolated in a gelatine capsule and allowed to produce either chrysopid or parasites. In this manner, a total of 10,812 *Chrysopa* cocoons was collected and individually recorded, together with an additional 1,500 cocoons from cotton-gin trash in the San Joaquin Valley.

HOST SPECIES

Of all the *Chrysopa* cocoons collected in various localities and on different host plants, with but one exception, only two species were obtained: *C. californica* Coq. and *C majuscula* Banks. The latter species has generally been considered rare, but I have found it to be exceedingly abundant in southern California. The single exception was an undescribed species[1] from walnut.

Both the larvae and adults of the species generally known as *C. californica* have shown pronounced variations which would seem to be of taxonomic significance. Early in the present study two distinct types of larvae were noticed, the adults of which were apparently identical except for the variable red facial

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[1] Chrysopidae determined by Roger C. Smith.

suffusion and the presence or absence of a black genal band. Figure 1 (A and B) separates the two larval types. The "Type 1" larva (A) is characterized by the narrow elongate black head markings and by its generally light body color and slender proportions. Adults reared from these larvae were divided by Smith into two groups, *Chrysopa harrisii* var. *externa* Hag., and *C. plorabunda* var. *californica* Coq. (see R. C. Smith, 1932). The "Type 2" larva (B) is dis-
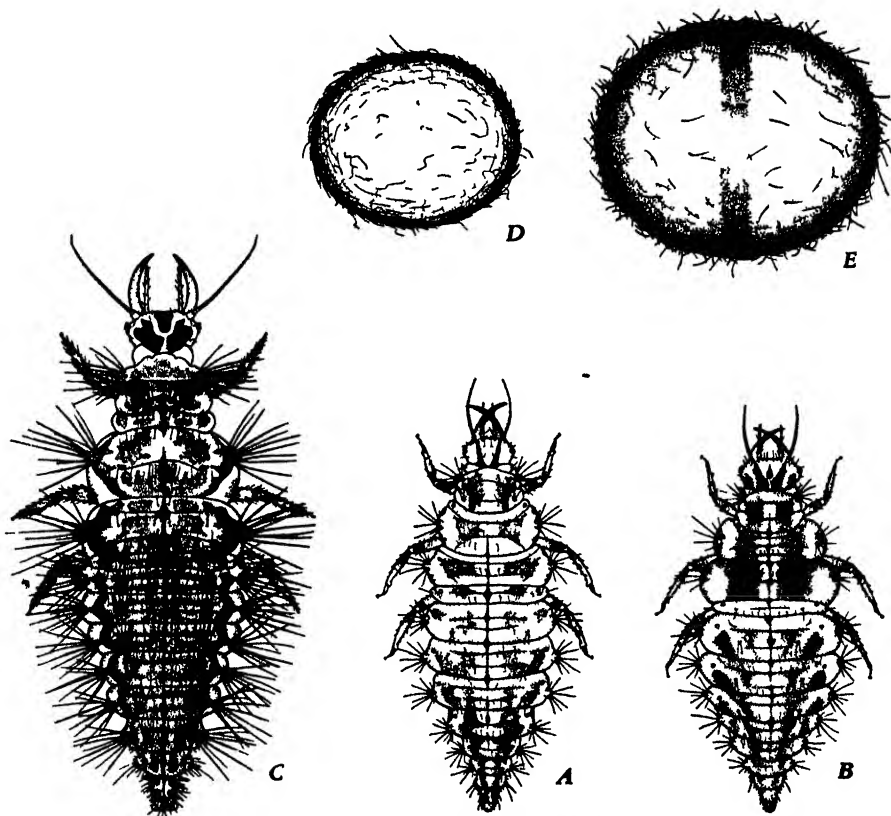
Fig. 1. Host species. A. Mature larva of *Chrysopa harrisii* var. *externa* Hag. and *C. plorabunda* var. *californica* Coq. (Type 1). B. Mature larva of *Chrysopa* n. sp. (♀) (Type 2). C. Mature larva of *C. majuscula* Banks. D. Cocoon of "*C. californica* complex." E. Cocoon of *C. majuscula*.

tinguished by an anterior black spot between the much wider longitudinal head markings, in addition to being considerably darker in color and of broader proportions. No intermediate forms were encountered; the types are apparently distinct. Smith has tentatively considered the adults reared from Type 2 larvae as either a new species or as one of several Mexican or West Indian forms heretofore unknown in California.

The two types of larvae were approximately equal in abundance, and, except as noted in a subsequent section, parasitized by the same species. For present purposes and in order to avoid confusion, the older name *C. californica* will be used throughout to designate this complex assemblage of forms.

The mature larva and cocoon of *C. majuscula* (fig. 1, C and E) are immediately distinguishable from those of *californica*. Both stages are in size nearly double those of *californica;* and the three angular larval head markings, the blackish metathoracic lateral tubercles, and the broad body will identify the larvae. The cocoon is oval with a more or less distinct dark band encircling the middle, and the walls are much thicker than in *californica*, the cocoon of which is semitransparent and papery in texture. Information on comparative abundance, host-plant preference, and so on, is presented in a later section.

PARASITE SPECIES REARED

A total of fifteen species was reared during the investigation.

(1) Heloridae
    1. *Helorus paradoxus* Prov.
(2) Encyrtidae
    2. *Isodromus niger* Ashm.
    3. *Isodromus iceryae* How.
    4. *Chrysopophagus compressicornis* Ashm.
(3) Perilampidae
    5. *Perilampus chrysopae* Cwfd.
(4) Eulophidae
    6. *Tetrastichus chrysopae* Cwfd.
(5) Pteromalidae
    7. *Pachyneuron californicum* Gir.
    8. *Dibrachys cavus* Wlk.
(6) Eupelmidae
    9. *Arachnophaga picea* (How.)
(7) Trichogrammatidae
    10. *Trichogramma embryophagum* (Htg.)
(8) Ichneumonidae
    11. *Hemiteles tenellus* (Say)
    12. *Chrysopoctonus patruelis* Cushm.
    13. *Gelis* sp.
(9) Cleridae
    14. *Hydnocera scabra* Lec.
    15. *Hydnocera affiliata* Fall

Eight families and twelve genera of the parasitic Hymenoptera are thus represented, in addition to a single coleopterous genus. Five species, *Isodromus niger*, *I. iceryae*, *Helorus paradoxus*, *Tetrastichus chrysopae*, and *Perilampus chrysopae* parasitize the active larval stages of *Chrysopa;* and all of them, except for the egg parasite, *Trichogramma embryophagum*, emerge from the host cocoon. The remaining species oviposit through the *Chrysopa* cocoon. *Hydnocera* spp., although normally predatory in habit, will occasionally mature upon a single individual, thereby assuming a truly parasitic existence. In such instances the newly hatched larva enters the *Chrysopa* cocoon, where it develops to maturity.

Despite repeated attempts, none of the primary parasites of either host was ever reared from the other species. The following tabulation emphasizes this unvarying relationship.

FROM *Chrysopa californica*

PRIMARY PARASITES	HYPERPARASITES
Isodromus iceryae	*Chrysopophagus compressicornis*
Perilampus chrysopae	*Pachyneuron californicum*
Tetrastichus chrysopae	*Dibrachys cavus*[a]
Trichogramma embryophagum	*Arachnophaga picea*
Chrysopoctonus patruelis	*Hemiteles tenellus*[a]
Gelis sp.	
Hydnocera scabra	
Hydnocera affiliata	

FROM *Chrysopa majuscula*

PRIMARY PARASITES	HYPERPARASITES
Isodromus niger	*Chrysopophagus compressicornis*
Helorus paradoxus	*Pachyneuron californicum*
	Dibrachys cavus[a]

FROM *Eremochrysa punctinervis* (McL.) (Laboratory parasitization)

PRIMARY PARASITES

Isodromus iceryae
Chrysopoctonus patruelis

[a] Reared also as a primary parasite; predominately hyperparasitic.

BIONOMICS OF PARASITES

HELORIDAE

Helorus paradoxus Prov.

The family Heloridae is paleontologically an extremely old one, being represented by the genus *Mesohelorus* in Turkestan formations of the Jurassic period (Martynov, 1925). The earliest known true Hymenoptera are found in strata of similar age (Imms, 1931). Brues has described *Serphites paradoxus* from Canadian amber, illustrating the wing, and also that of *Helorus;* the two are very similar. As originally established by Ashmead, the Heloridae consisted of two subfamilies and the three genera, *Helorus, Ropronia,* and *Monomachus.* Crawford (1909) has since erected the family Vanhorniidae to accommodate a most peculiar new species which is similar in many respects to *Helorus.* The confusion which still exists within this group of archaic forms illustrates the need for biological information as a necessary adjunct to systematics.

The first reference to a species now recognized as *Helorus* is Panzer's (1798) description of *Sphex anomalipes.* Latreille in 1802 erected the genus *Helorus* with *H. ater* as the type (now synonymized with *H. anomalipes,* although *ater* was subsequently named from different specimens). As early as 1807 Jurine in France illustrated *H. ater* in detail. Seven species are recognized by de Dalla Torre (1898), with three additional species since recorded. Bradley's *H. chrysopae* (see R. C. Smith, 1922) is apparently undescribed in the literature; it was probably *H. paradoxus.*

So far as known, *Helorus* is parasitic only on the Chrysopidae. Except for the present species all are exotic. The genus is predominantly European in distribution, although *H. striolatus* and *H. brethesi* are listed from India and

South America, respectively. *H. corruscus* has been reared from *Chrysopa flava*, *C. ciliata*, and *C. ventralis* in England; *H. rugosus* from *C. septempunctata* in England; *H. anomalipes* from *C. flava* (?) also in England, and from *C. vulgaris* in France. "*H. chrysopae*" is recorded from *C. oculata* (?) in New York; and the only known host of *H. paradoxus* is that listed by the writer, namely, *C. majuscula*. McGregor and McDonough's (1917) reference to *Helorus* sp. from *C. rufilabris* in South Carolina is probably *H. paradoxus*. The majority of parasite references are unaccompanied by specific host records, as exemplified by Provancher's original description of *H. (Copelus) paradoxus* (1883).

Relatively little information exists on the bionomics of the Serphoidea, and particularly on the family Serphidae (Proctotrupidae). Eastham's account (1929) of *Phaenoserphus viator* Hal. and a paper by Zolk (1924) on *Paracodrus apterogynus* Hal. are apparently the only publications dealing with the biology of the Serphidae. The present account is the first on the Heloridae.

The Adult.—The adult female (fig. 2) is shining black, the thorax characteristically punctate and sculptured posteriorly, and the face with sparse whitish pubescence. Petiole rugose with raised longitudinal lines above. Length 4.5 mm. *H. paradoxus* was the largest species reared from *Chrysopa*.

Although rather excitable, the adults are easily kept in the laboratory. Females are longer lived than males, but considerable variation was noted with different individuals. Under the same conditions longevity ranged from 8 to 51 days, the average about 25 days.

Host Specificity.—Although *H. paradoxus* never emerged from field-collected *C. californica* cocoons, and laboratory oviposition could not be induced under normal conditions, it was found that by smearing the larvae with the body fluids of crushed *C. majuscula* larvae, deposition could be obtained as readily as with the normal host. Unfortunately, only a few *C. californica* larvae were thus parasitized, so that the information obtained is somewhat scant. Eclosion and larval development occurred normally throughout the first instar, and metamorphosis was also inhibited until the *Chrysopa* cocoon had been spun. A second-instar larva was dissected from the one remaining parasitized host.

Oviposition.—Oviposition may be effected within several hours of emergence, although occasional females required a preoviposition period of 2 to 8 days. *Chrysopa majuscula* larvae of all sizes are attacked with almost equal readiness. Following a brief antennal examination of several seconds, the abdomen is suddenly brought forward beneath the thorax and the very short ovipositor jabbed forcibly into the host. Almost invariably the lateral or ventrolateral region of the larva is chosen, generally in the posterior half of the body. This causes the host to run away, dragging the motionless parasite along. Once the ovipositor is firmly imbedded, the female relaxes with little or no movement until the act is completed. The entire procedure occupies 9 to 27 seconds. A single egg is deposited at each insertion, although occasionally the act is performed without an egg being laid.

A female which lived 49 days and commenced oviposition on the fourth day, deposited a total of 25 eggs within 35 days. Rarely more than a single egg per day is deposited even though the ovaries generally contain a variable

number of mature ova. The same female contained 24 fully developed ovarian eggs after death; various other records also indicate an average reproductive capacity of approximately 30 to 50 eggs per female. Oviposition is most rapid during the first half of adult life.
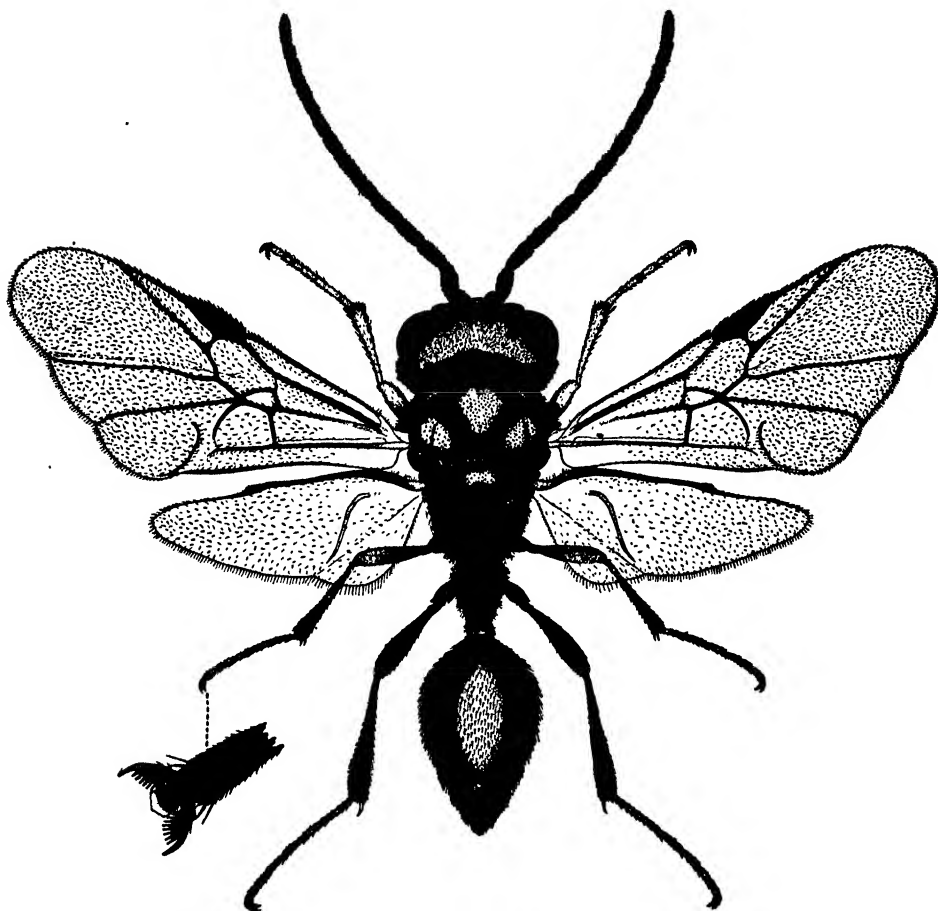
Fig. 2. *Helorus paradoxus* Prov. Adult female showing tarsal comb.

Egg.—The glistening whitish egg (fig. 3, A) is deposited free within the body cavity of the host. A minute protuberance, apparently the micropyle, occurs at the broad end. After about 24 hours the egg begins gradually to increase in size owing to absorption of host fluids. The trophic membrane is now faintly discernible beneath the chorion. The details of this membrane, however, are very faint even just before eclosion (fig. 3, B); numerous rings of tiny bubbles sometimes appear as in *Chrysopophagus compressicornis*. An increase in size from 0.33 mm. by 0.13 mm. when newly deposited to an average maximum of 0.47 mm. by 0.28 mm. was noted. The egg more than doubles in width although increasing slightly less than one-half in length.

The curled embryo lies with the head at the broad or "micropylar" end.

When mature it squirms about very actively; the head capsule generally assumes a faint melanization prior to eclosion.

Incubation requires 2 to 5 days depending upon the temperature. At 75° F. hatching occurred in 3 days.

Larvae: first instar.—The primary larva (fig. 3, C) is a most peculiar individual in many respects. The elongate, 13-segmented body bears ventrally a pair of fleshy pseudopods on each of the abdominal segments except the last one which ends in a distinct tail; the ninth pair are vestigial and sometimes cannot be distinguished. The heavily chitinized, brownish head capsule is
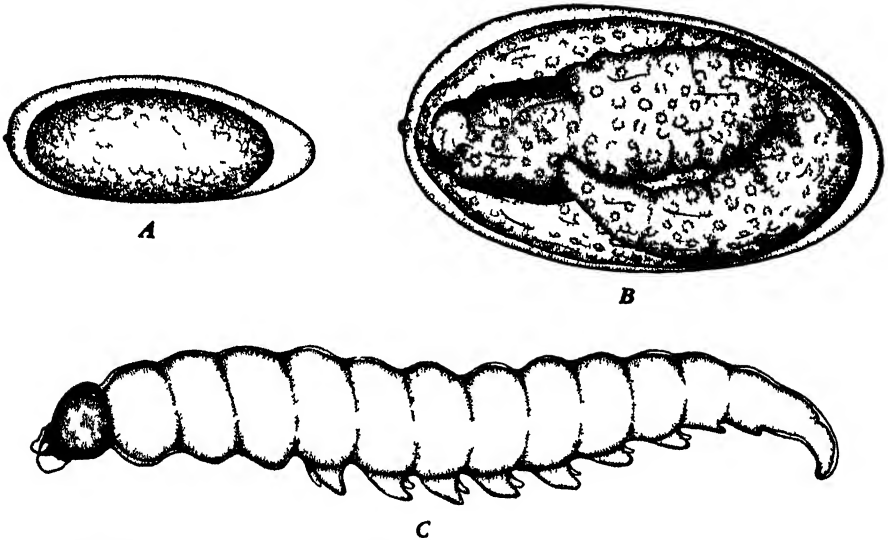
Fig. 3. *Helorus paradoxus* Prov. A. Newly deposited egg. B. Egg showing mature embryo within trophic membrane C. First instar larva, one day old.

always prominent, particularly with newly emerged larvae when it is nearly equal in diameter to the body. Anteriorly it bears an extremely delicate, membraneous sac (fig. 4, A) within which the large, chitinized mandibles (fig. 4, B) are contained. The mandibular articulation appears as a thin whitish line, and the anterior rim of the head capsule is thickened and coal black in color. Even slight pressure will cause the mandibles to break off at the basal articulation. The oral aperture is extremely minute and generally indistinguishable. Several pairs of microscopic papillae occur on the surrounding surface. This peculiar oral sac is otherwise absolutely structureless and transparent, being the only nonsclerotized portion of the head capsule.

The head capsule averages 0.160 mm. in width, and the mandibles 0.062 mm. in length. The head and tail are deflected somewhat ventrally, and the larva is able to curl itself into a complete circle.

Most internal organs and structures are readily observed through the transparent derm (fig. 4, C). The long, tubular gut may be traced to a point on the dorsum just above the tail. Ventral ganglia occur in all but the last two segments; the eleventh ganglion is larger than the preceding ones, whereas the

supraoesophageal ganglion occupies a large portion of segment 1. The respiratory system is vestigial and exceedingly difficult to trace even at high magnifications. The lateral trunks never extend beyond segment 6 and generally terminate in segment 4 or 5; lateral tracheae are short and unbranched, and there is no posterior commisure.

Although very active when newly emerged, the mature larva becomes almost motionless. An average increment of 0.90 mm. by 0.16 mm. at eclosion
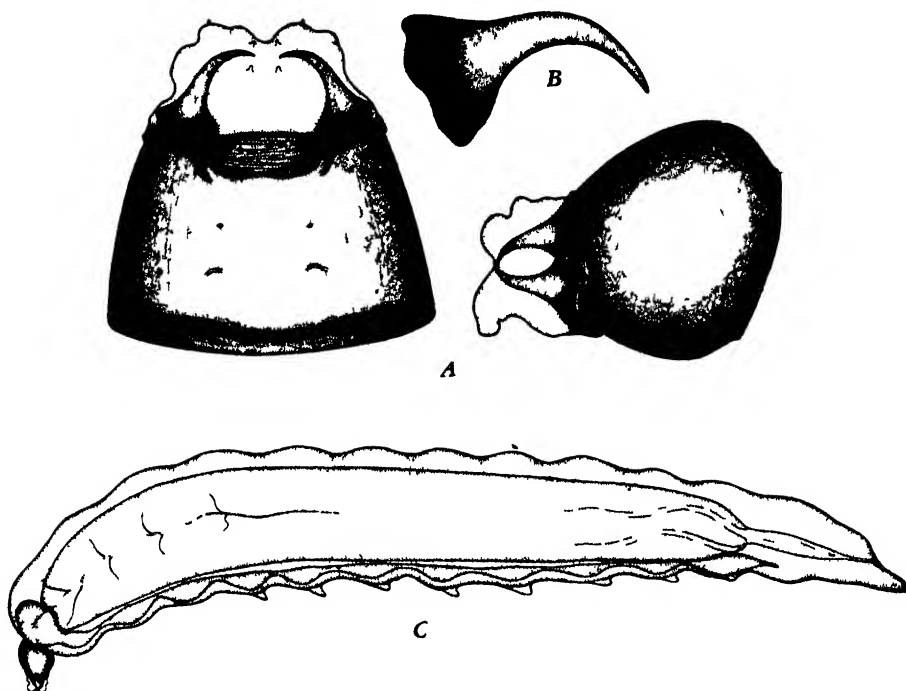
Fig. 4. *Helorus paradoxus* Prov. A. First instar head capsule, ventral and lateral aspects. B. First-instar mandible. C. Mature first-instar larva prior to molt

to 2.34 mm. by 0.39 mm. when fully fed was noted. The largest individual measured 2.70 mm. in length.

Pseudopod-bearing primary larvae of this general type are also known in the Serphidae, Cynipidae, Ichneumonidae, and Braconidae. The primary larva of the serphid *Phaenoserphus viator* (Eastham, 1929) most nearly resembles *Helorus* to which it is closely related. Several parasitic cynipids of the genera *Ibalia* (Chrystal, 1930), *Cothonaspis, Figites, Kleidotoma* (James, 1928), and *Eucoila* (Keilin and Pluvinel, 1913), in addition to the ichneumonid *Collyria calcitrator* Grav. (Salt, 1931) and the braconids *Microdus pumilus* Rtz. (Thorpe, 1933) and *M. dimidiator* (Silvestri, 1923), also possess paired pseudopods. In the cynipids (except *Ibalia*) eclosion occurs at an earlier embryonic stage (Berlese's protopod stage) as evidenced by the absence of abdominal appendages; in the first-instar larvae of *Ibalia, Helorus, Phaenoserphlus, Collyria,* and *Microdus,* however, pseudopods arise from the abdominal seg-

ments, and in several, from all or part of the thoracic segments as well, thus denoting a modified polypod stage.

It is commonly agreed that eggs which are poor in yolk hatch at an early stage of embryonic development. Generally associated with this phenomenon is the presence of a more or less distinct trophic membrane, and, in primary larvae, the complete absence or great reduction of the tracheal system. *H. paradoxus* is the only one of the aforementioned species which possesses any sort of tracheal system during the instar.

The first instar of *Helorus* varies greatly in duration according to the season and to the metamorphosis of its host. The initial molt never occurs before the *Chrysopa* larva has entered the prepupal period, and the parasitized host is never allowed to pupate. A number of parasitized larvae were fed barely enough to maintain life without permitting them to spin; in this manner primary larvae were dissected as late as 17 days from oviposition, although the instar normally averages but 4 days when the host has spun before *Helorus* is ready to molt. Overwintering also occurs as full fed primary larvae. In both instances larval growth continues normally until the maximum size is attained, followed by a resting period which may be terminated only by host spinning or by the ending of the diapause. Overwintering *C. majuscula* were placed in the insectary at a constant temperature of 80° F. Premature host and parasite emergence resulted in about one-half the time normally required, although the diapause could not be entirely eliminated.

A portion of the overwintering *C. majuscula* generation fail to emerge until the second year. Parasite development is similarly inhibited within such individuals. *Helorus* is therefore able to remain in the first instar for nearly two years without apparent change.

Several parasitized *Chrysopa* larvae entered the prepupal period without constructing cocoons, but after a brief interval parasite development proceeded in the usual manner.

Second instar.—The second-instar larva (fig. 5, A) is totally unlike that of the previous stage. There are no pseudopods, the sclerotized head capsule has disappeared, and the tail is greatly reduced. The anus is now terminal in position instead of dorsal, and no mandibles of any kind could be distinguished. The mouth is seen ventrally as a faint transverse slit just below a pair of rounded swellings, being bordered on each side by a smaller convexity. A remarkable advance is shown in the tracheal system; minute spiracular spurs appear in many of the body segments, and the lateral trunks now extend the entire length of the body, giving rise to extensive dorsal and ventral branches which end in tiny arborizations throughout the body. There is still no posterior commissure.

In *Phaenoserphus*, as with *Helorus*, the mandibles are either vestigial or lost in the second instar. The pseudopods have also disappeared in both species.

A most unusual and apparently heretofore undescribed structure (or rather, series of structures) was invariably found within the midgut of second- (and third-) instar *Helorus* larvae. Partially grown second-stage larvae exhibited a series of curious membranous sacs which may be readily dissected from the

lumen of the midgut (fig. 6, A). There are usually 5 distinct sacs, each within the next larger one, and the midgut walls (not shown) fit closely about the outer layer. A definite cellular neck attaches the whole internally at the junction of fore and midgut, the entire series of closed sacs being thus suspended without additional attachment. Because of their homogeneous noncellular character, point of origin, and contained food materials, each sac is apparently
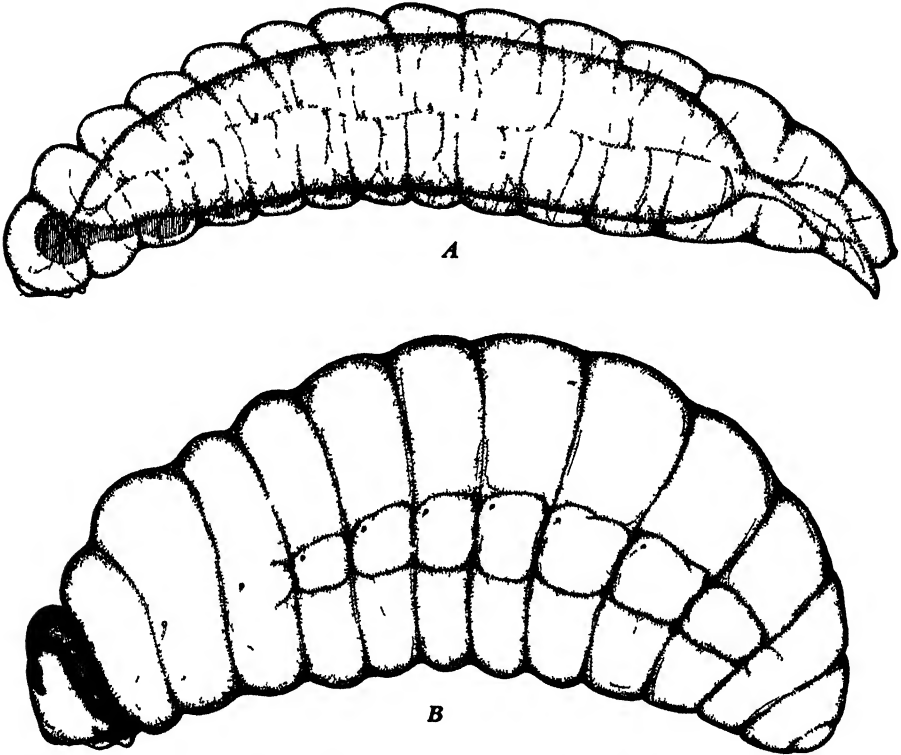
Fig 5. *Helorus paradoxus* Prov A Second instar larva B. Third instar larva just before leaving host.

homologous with the peritrophic membrane found in many insects, and the term "peritrophic sac" will be used to designate each of these structures.

The innermost sac, which appears to communicate directly with the opaque whitish neck, is filled with a thick yellowish curdlike substance, and the others are progressively more transparent because of the less dense watery materials which they contain. The outermost peritrophic sac contains a very thin watery fluid which is but faintly greenish yellow in color; inside it sac 2 is distended with a dark-green liquid of slightly greater density, and the intervening sacs (no. 4 often being indistinct) are generally somewhat wrinkled and more or less transparent in nature. If the larva is pressed firmly beneath a cover slip, the entire apparatus suddenly bursts free, always breaking at the same point in the neck. The walls of the midgut are thick and very elastic; when the peritropic sacs are released they immediately contract into a shapeless whitish mass.

Newly molted individuals at first lack all but two of these membranes. A very small nearly transparent sac occurs within a second much larger one containing a pale-green fluid. The small sac apparently receives the ingested food, whereas the larger one appears identical with the outermost membrane described above. The order in which the others arise was not ascertained.

Parker (1931) has described a peritrophic membrane in *Macrocentrus gifuensis* Ashm. larvae which is closed posteriorly to form a complete sac. This sac gradually extends until it fills most of the midgut. Although no additional membranes are shown, the surrounding food materials are definitely arranged
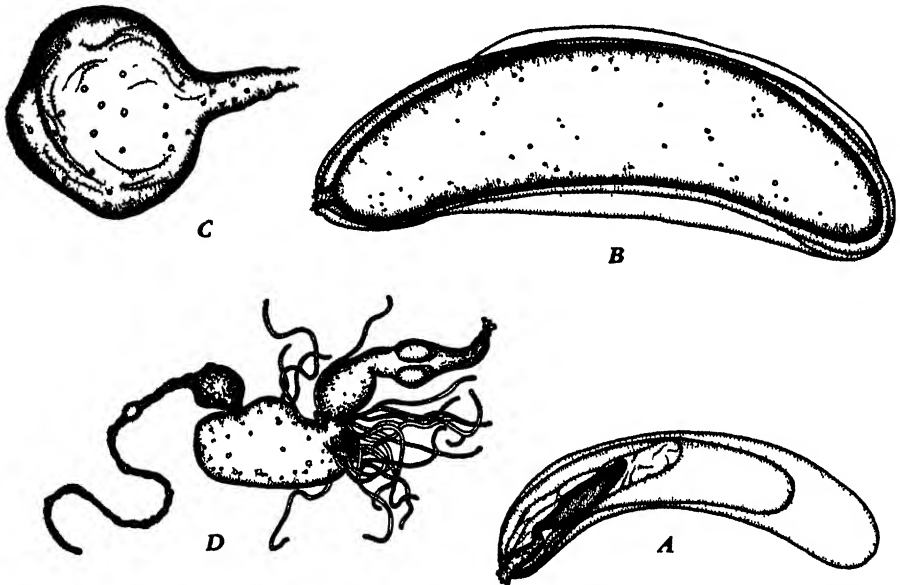
Fig. 6. *Helorus paradoxus* Prov. A. "Peritrophic sacs" dissected from midgut of mature second-instar larva. B. Same from midgut of third-instar larva before leaving host. C. Same from mature third instar just before pupation, showing "urate bodies." D. Alimentary tract from pupa showing reduced food mass in midgut. (All drawn to same scale with camera lucida.)

into two zones with respect to density and character, just as in early *Helorus* larvae. The innermost peritrophic sac of *Helorus* is apparently identical with that of *M. gifuensis*.

Beginning soon after the initial parasite ecdysis, the host blood becomes increasingly filled with small, opaque, spherical white bodies which spew out and sink to the bottom when the *Chrysopa* is opened. As they increase in number, the fat bodies and softer tissues become shrunken. The origin of these bodies could not be determined; they were also invariably found within the alimentary tracts of second and third instar *Helorus* larvae.

The host remains alive until the following molt, although about midway in the instar all movement ceases. Only the pulsating dorsal vessel is indicative of life. Toward the end of the parasite instar the whitish bodies may be faintly perceived through clear areas in the host derm and in the feebly circulating

blood as it passes through the dorsal vessel. The stage of the parasite may be accurately judged from these outward indications.

There are 3 Malphigian tubules all of equal length; although strongly convoluted, when extended they are considerably longer than the larva itself. Each tubule is attached in the usual manner, rather than originating from a common duct as described by Eastham for *Phaenoserphus*.

Maximum dimensions average 5.20 mm. by 1.26 mm. at the end of the instar, the larva having more than doubled in size in 2½ to 5 days (3½ days at 75° F.). It then occupies somewhat more than one-half the body of its host.

Third instar.—In this, the final instar, the larva passes through several morphological phases which merge imperceptibly one into the other. The newly molted larva is noticeably shorter but broader; average measurements are 4.0 mm. by 1.50 mm. The host is invariably killed at this point. Eight pairs of spiracles are present on the anterior margins of segments 2 to 9 inclusive, and paired spiracular spurs end blindly in segments 10 and 11. The full complement of eight pairs is constant throughout the instar, and the blind spurs also remain undeveloped. As in both *Phaenoserphus* and *Collyria*, there is never a posterior commisure.

The host body contents are generally entirely consumed in 48 hours, leaving the *Chrysopa* derm tightly enfolding the larva. Prominent lateral swellings have developed, the derm is very minutely roughened, and the head has assumed a most peculiar dark brown melanized band encircling the lateral posterior margins (fig. 5, B). It first appears faintly within 24 hours, becoming complete as the host fluids disappear. The process is apparently oxidative in nature, since newly molted individuals acquire this characteristic melanization within several hours when exposed to the air. There is no trace of sclerotization.

With but one exception, each larva was oriented with the head toward the posterior end of its host. After remaining full fed within the *Chrysopa* skin for an average of 2½ days, the larva partially emerges near the caudal extremity, finally coming to lie with the last four or five segments still embedded (fig. 7, A). The eighth pair of spiracles may be either free or covered by the host derm. Very soon the thoracic segments commence to bulge dorsally and smaller transverse swellings appear in the center of each abdominal segment. Shortly before pupation their maximum development is attained; the swellings of the thorax differ in arising longitudinally from the middorsal region, being somewhat reminiscent of a cock's comb. Except for the lateral ridges and melanized cephalic areas, neither of which was present at the beginning of the instar, the larva now presents an entirely different appearance. The pupal eyes appear in the first segment as pale-red discs just beneath the epidermis.

The facial region of the mature larva (fig. 7, B and D) presents certain interesting features. The transverse slitlike mouth is bordered on either side by the vestigial mandibles which arise from circular swellings; only the minute points are sclerotized (fig. 7, C) and they are completely nonfunctional. Just beneath, the maxillae also appear as rounded swellings, and are surmounted by 4 tiny sensillae (?), two of which are dark in color. The aforementioned melanized

·band, apparently unique with *Helorus*, borders the mandibular bases. The antennal papillae are separated by a shallow depression. The mouth parts of *Phaenoserphus* are nearly identical in most respects; this extremely simplified type is apparently otherwise undescribed among the parasitic Hymenoptera.

In the final instar the peritrophic sacs are the same in number but greatly enlarged (fig. 6, B). Sac 4 (from the outside) is apparently the one now in direct communication with the neck, and has become greatly distended with semisolid cream-colored material consisting mainly of the opaque rounded bodies described in connection with the second instar. The small innermost sac
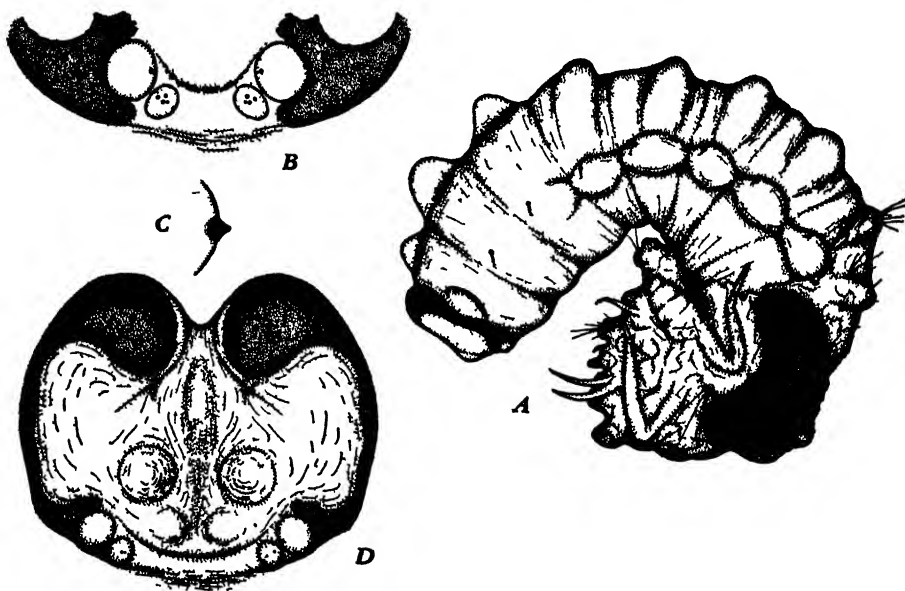
Fig. 7. *Helorus paradoxus* Prov. A. Mature third instar larva just before pupation, showing caudal region imbedded in host remains (note black bean-shaped host meconium). B. Third-instar mouth parts, showing transverse slitlike mouth, vestigial mandibles, and maxillae. C. Greatly enlarged mandible. D. Facial region of same showing melanized areas, larval antennae, and mouth parts.

is contained within it as before, being entirely obscured by the surrounding material. Immediately prior to pupation the food mass undergoes considerable compression and reduction in volume (fig. 6, C). Numerous white urate bodies appear scattered over the surface. The membranes are then individually indistinguishable, although if soaked in water they gradually unfold until their former appearance is largely restored. The brownish-tan mass was always forced into the posterior half of the body.

A possible explanation for this complex apparatus appeared when it was discovered that the meconium is retained within the pupa. Consequently there is no true prepupal stage in *H. paradoxus*. When dissected from the pupa, the digestive system appears as in figure 6, D. The waste material has been reduced in bulk by the elimination of liquid. The peritrophic sacs apparently function as a sort of filter chamber which subtracts the fluids, thus leaving only solid residue to be carried over into the pupa. The abnormally developed

Malphigian tubules and midgut epithelium, together with the presence of urate bodies and peritrophic sacs, all of which are involved in digestion and excretion, seem to indicate an unusual interrelationship. The conclusion that all of these structures are in some way also related to·the peculiar type of food material likewise appears inescapable.

An average of 3½ days is passed in a quiescent state after emerging from the host; this interval replaces the usual prepupal stage. Although the third instar occupies about 8 days in all, the feeding period generally terminates at the end of the second day. The largest mature individual measured 7.00 mm. by 2.15 mm.; the average length is about 6.25 mm.

Pupa.—At the last molt the caudal region is withdrawn from the enveloping host derm, the pupa remaining but lightly attached at the tip. Unlike *Phaenoserphus*, there are no caudal hooks to anchor it in place. Very frequently the larval skin is incompletely shed, and remains more or less overlying the head of the pupa.

The pupae range from 4 00 mm. to 5.50 mm. in length, and lie curled to fit the walls of the host cocoon. Larvae which were dissected out and allowed to pupate free also assumed this position. Emergence follows a pupal stage of 8 to 12 days, depending upon the temperature. The adult cuts a distinctive type of exit hole which is at once distinguishable from those of other *Chrysopa* parasites. Beginning toward the center, an irregular, continuous circular cut is made which gradually widens corkscrew fashion (see R. C. Smith, 1922, fig. 160, C). The incised operculum thus created remains attached at one side.

Cocoons from which *Helorus* had emerged showed no trace of the larval meconium. It is therefore either ejected during the life of the adult or permanently retained within the abdomen.

Sex Ratio.—Exact figures are not available. From a total of 45 adults reared from field-collected *C. majuscula* cocoons, however, only several males were recognized. The sexes of *H. paradoxus* are distinguished with difficulty. Females seem to greatly outnumber the males.

Superparasitism.—Oviposition will occur repeatedly by one or more females in the same host individual. Unlike any other *Chrysopa* parasite the supernumerary larvae are frequently attacked, generally by the individual which was first to hatch. A large series of *C. majuscula* larvae were parasitized two to five times each at various intervals. Some were allowed to spin cocoons, and others were dissected as larvae. The following discussion summarizes the data thus accumulated.

Since *Helorus* possesses functional mandibles only in the first instar, its cannibalistic proclivities are limited to that stage—3 to 6 days in duration providing the host has spun. Toward the end of the instar, however, the larva becomes so distended and sluggish that it is unable to attack as before. If another larva hatches at that time or subsequently, it develops until the host contents are consumed, for the most part by the older individual. The supernumerary larva is then "starved out," leaving the prior inhabitant to mature. Occasionally, however, larva no. 2 attacks its defenseless·companion and itself reaches maturity. Quite frequently one or more supernumerary larvae escape, so that

eventual starvation is the final limiting factor. Only one parasite ever matures per host. Cannibalism has also been recorded in *Collyria; Phaenoserphus* is a gregarious species.

There is some evidence that when competition is involved larval development is retarded. For example, 3 females oviposited in rapid succession within a single *Chrysopa* larva which cocooned after 18 days. Six days later the host was dissected, yielding 3 live *Helorus* larvae, one of which was a full-fed second instar, another a newly molted second instar, and the third a mature first-instar larva. Although of the same age, the extremes were an instar apart. The most advanced individual was approximately normal, whereas the others lagged behind. It will also be noted that the smallest larva showed no progress whatever during the 6 days following spinning.

Primary larvae which have been killed through cannibalistic attack are generally encysted by the living host. The extent of encystment depends upon the interval which elapses before the host is killed. Where parasitized *Chrysopa* larvae remained for many days before spinning, complete encapsulation resulted. The brown head capsule was always distinguishable within the oval whitish cyst. Encystment is usually accompanied by a blackish discoloration of the engulfed object.

Superparasitism is probably infrequent in the field. Natural parasitism by *Helorus* has always been relatively low. The species is apparently one of the rarer parasites of *Chrysopa*.

Life Cycle.—The following figures apply to normal metamorphosis only, as previously explained.

Life cycle	Extremes	Averages
	days	*days*
Egg	3 0– 5 0	4 0
First instar	3 0– 6 0.	4.0
Second instar	2 5– 5.0.	3 5
Third instar	6 0–10 0.	8 0
Pupa	8 0–14 0.	10 0
Total	22.5–40 0.	29 5

H. paradoxus was the only species to overwinter as immature larvae, a characteristic also shared by both *Phaenoserphus* and *Collyria*.

ENCYRTIDAE

Isodromus niger Ashm.

I. niger was originally described from a female captured while ovipositing in a chrysopid larva (Ashmead, 1900) in Washington, D.C. It has since been recorded from *Chrysopa oculata* Say in Wisconsin and from "*Chrysopa* spp." in California, Utah, and Massachusetts. A single exotic record lists this species from Fórmosa. The rearing of *I. niger* from *C. majuscula* is herein noted.

Several host records which must be considered doubtful include *Symphero-*

bius angustus (Banks), "hemerobiid cocoon," and *C. californica.* Although I reared numerous hemerobiid parasites, none of the *Chrysopa* primary parasites ever issued from brown lacewings. *I. niger* could not be made to parasitize hemerobiid larvae in the laboratory and evinced but slight interest in them.

The Adult.—The adults (fig. 8) are readily distinguishable from those of *I. iceryae* How. by their generally black coloration in contrast with the striking
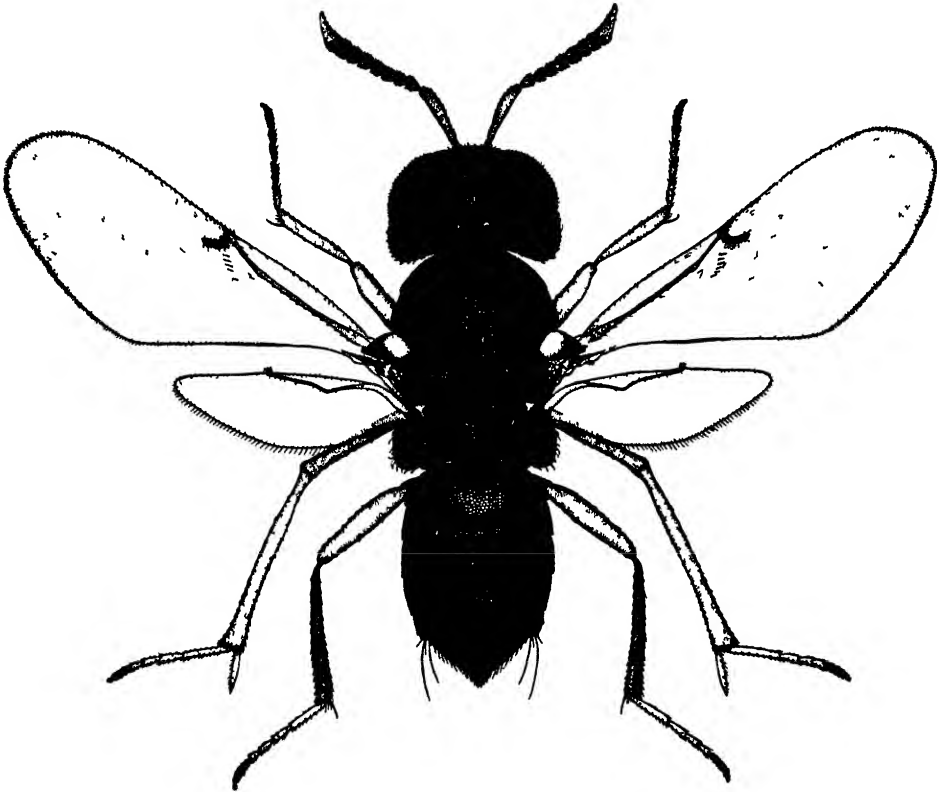
Fig. 8. *Isodromus niger* Ashm. Adult female.

yellow and black pattern of the latter species. In addition, the tegulae are white-banded and the middle and hind tarsi whitish; the males have a greater part of the face primuline yellow Timberlake (1919) has redescribed the species in detail.

Host Specificity.—A remarkable specificity exists among the primary parasites of *C. californica* and *C. majuscula. I. niger* will parasitize only the latter species. *C. majuscula* larvae were crushed and the larval skins and body fluids deposited on *C. californica* larvae in an effort to induce oviposition, but with negative results.

According to Smith's classification of the Chrysopidae, using both larval (Smith, 1922) and adult (Smith, 1932) characters, *californica* clearly runs to his "*plorabunda* section" in both cases. I have made a detailed study of the

immature stages of *C. majuscula*,[2] the larva unmistakably belongs in Smith's "*nigricornis* section" adjacent to *C. nigricornis*. Smith (1932) has assigned the adult of *majuscula* to his "rufilabris section," admittedly a somewhat heterogenous group, although he noted its close resemblance to *C. nigricornis*. It would, therefore, appear that *C. majuscula* correctly belongs in the "*nigricornis* section" of the genus *Chrysopa*. *C. oculata*, the only other valid host of *I. niger*, is also near to *C. nigricornis* in Smith's classification of larvae.

The two species, *californica* and *majuscula*, are thus at opposite ends of the genus. Host-parasite specificity, at least with those species investigated, seems remarkably correlated with this natural division. Further information is needed in order to ascertain the extent of this specificity among more closely related species.

Oviposition.—Following a brief and rather cautious examination of the host by the female, the abdomen is brought forward between the legs until nearly parallel with the body, the exserted ovipositor reaching considerably beyond the head. In this position the eggs are deposited. The host larvae often run away from the ovipositing females or lash about in an attempt to seize them with their mandibles. The parasites, however, are usually adept at dodging and immediately return to the attack. Although the host is approached carefully from the rear, and the ovipositor is inserted rather deliberately, the *Chrysopa* larva sometimes captures its tormentor. The parasite is then impaled upon the mandibles and raised in the air while its body fluids are consumed.

Oviposition may commence within several hours of emergence. Newly emerged females contain mature eggs and oviposition generally begins during the first day. The eggs are laid in clusters of 1 to 7 at a single insertion of the ovipositor, and there may be a variable number of clusters per host. In the field, however, a single oviposition per larva is probably the rule. In the laboratory the average number of eggs per cluster was 4. A reproductive capacity of about 40 to 60 eggs per female is indicated.

Mature larvae are preferred for oviposition although second-instar larvae are also acceptable. Deposition generally occurs in the posterior two-thirds of the body in the lateral or ventrolateral regions, although eggs may often be found elsewhere.

Larvae of *Eremochrysa punctinervis* (McLach.) were offered, and the females were several times observed briefly to insert their ovipositors, although no parasites issued from the cocoons. An attempt was also made to secure oviposition in active *C. majuscula* prepupae, but without success.

Egg: ovarian egg.—The ovarian egg is of the usual double-bodied type common in the Encyrtidae. The average measurements follow.

Length of egg body	0.18 mm.
Width of egg body	0.09 mm.
Length of neck	0.09 mm.
Length of bulb	0.27 mm.
Total length	0.55 mm.

Along the neck and for nearly three-fourths the length of the egg body (fig. 9), is a well-defined band which appears roughened or granular at high

[2] To be published.

magnifications, and which becomes heavily melanized upon exposure to the air or to the body fluids of the host. Maple (1937) has ascribed to it a respiratory function in conveying atmospheric air to the developing larva. Many authors have described metapneustic encyrtid larvae, but have concluded that air was obtained by means of the hollow eggstalk. In *I. niger*, as with Maple's species, the tip of this stalk was entirely closed after deposition by the shriveled and hardened ovarian egg bulb. Maple's theory that the "cells" of this "respiratory plate" serve to convey air to the immature stages is in close agreement with my findings.
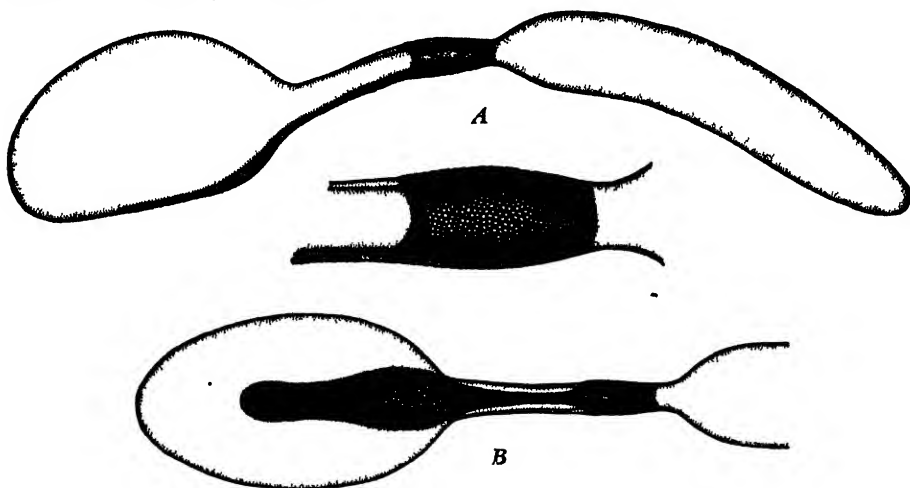
Fig. 9. *Isodromus niger* Ashm. A. Ovarian egg, lateral aspect, showing enlarged portion of "neck." B. Ovarian egg, ventral aspect.

It will be noted that the plate or band on the egg body is broadest and the cells are largest toward the base where the larval spiracles will ultimately lie and that a similar differentiation is apparent on the distal end of the neck which will project from the host following deposition. The narrow connecting band is composed of smaller cells and is considerably more limited in extent.

Deposited Egg.—Immediately after oviposition the ovarian egg bulb collapses to form a whitish mass on the tip of the stalk (fig. 10, A). The point at which the host derm is pierced soon becomes discolored and hardened, which assists in finding the egg cluster. Because of the short stalks, the eggs or young larvae are faintly discernible beneath as rounded whitish bodies. Melanization soon becomes apparent throughout the "respiratory plate." Ovarian eggs dissected from females which had been dead for several days showed a similar discoloration.

Larvae.—Three larval instars were definitely identified; a possible fourth instar may occur between the second and third.

First Instar.—At laboratory temperature eclosion generally occurs 2½ to 3 days from oviposition. The tracheal system is well defined in the mature embryo, but after feeding commences it is best studied in glycerine mounts. The larva is metapneustic with a single pair of open spiracles at the extreme pos-

terior end of the body in close apposition to the respiratory plate. Lateral tracheal trunks and commisures are present; the eight pairs of lateral branches are very minute.

The larva is almost spherical with no trace of segmentation, and the chorion with its pigmented band and attached stalk tightly encloses the posterior third of the body (fig. 10, A). Although generally found in clusters (fig. 10, B), single larvae are not uncommon. The respiratory plate is always uppermost, that
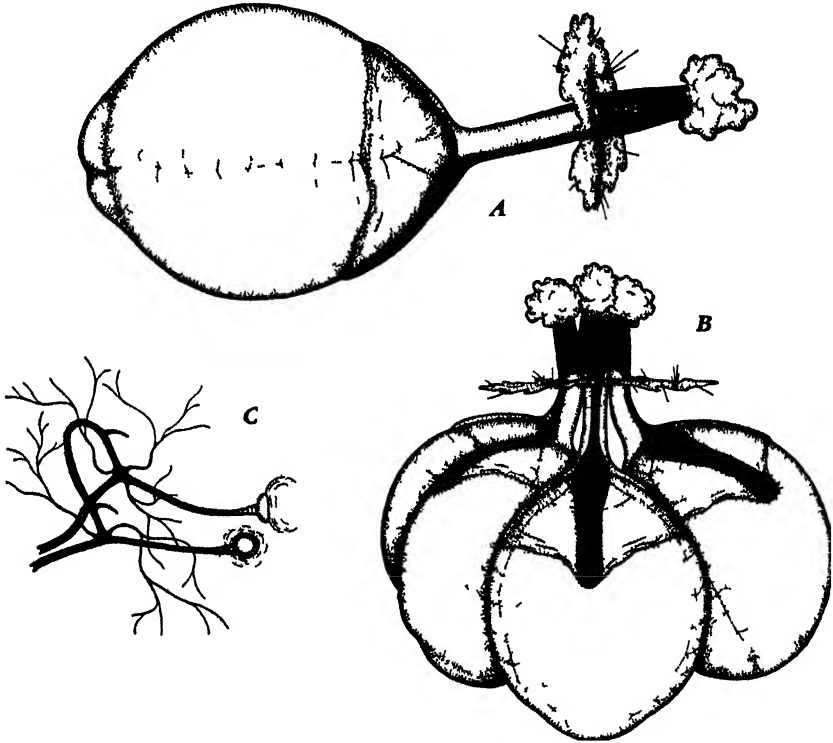
Fig. 10. *Isodromus niger* Ashm. A. First instar larva. B. Cluster of first instar larvae. C. Second instar larval spiracles showing "spurs" on posterior commisure

is, nearest the host derm. The stalks are tightly wedged into a single aperture where the hardening host fluids anchor them in position.

The mandibles (fig. 11, A) are extremely minute and semitransparent; the points measure barely 0.004 mm. in length.

At ecdysis the exuvia is sloughed off posteriorly and remains attached at the edge of the persistent chorion. The completion of the instar requires 1 to 1½ days, the larva increasing in size from 0.18 mm. by 0.15 mm. to 0.26 mm. by 0.21 mm.

Second Instar.—Segmentation is now distinct, except for the posterior region enclosed within the chorion. Usually 9 body segments appear anteriorly; the anal region is nearly smooth in outline. The tracheal system is unchanged except that eight pairs of spiracular spurs are apparent in segments 2 to 9 inclusive, which will connect with open spiracles in the following instar. In

addition, the tracheal ramifications are more extensive. When dissected from the enveloping anal attachment, the spiracles appear to lie within shallow cup-like depressions (fig. 10, C). A pair of peculiar tracheal spurs project from the posterior commisure; identical structures are also found in mature larvae.

During the second instar a very delicate, tightly fitting membrane is found adhering closely to the body, enveloping all but the head and most of segment 1. Its removal *in toto* is impossible because of its extreme fragility. Sections
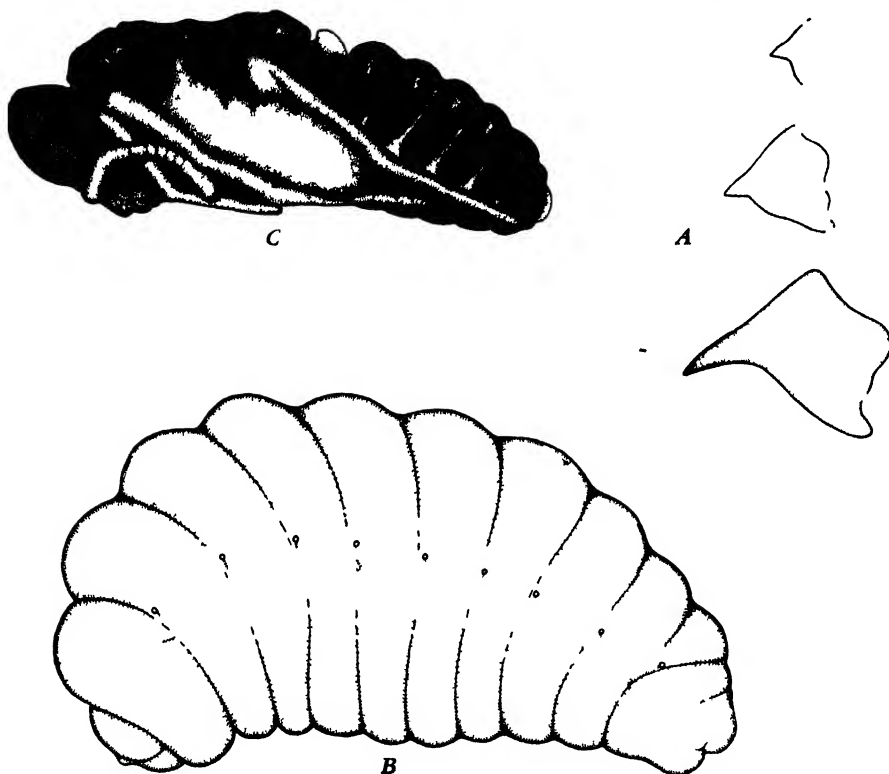
Fig. 11. *Isodromus niger* Ashm. A. Larval mandibles, first, second, and third instars
B. Mature third-instar larva. C. Mature pupa.

examined under high magnification have failed to exhibit any trace of cellular structure. Toward the end of the instar the membrane becomes minutely roughened. Further changes occur during the third instar.

The mandibles (fig. 11, A) now average 0.030 mm. in length; the points measure 0.008 mm. Although somewhat larger in size, they are still semi-transparent and nonmelanized.

The larva becomes disengaged from its posterior attachment at ecdysis, remaining free within the host throughout the remainder of the larval period. The duration of the second instar is 2 to 3 days, the larva increasing in size from 0.27 mm. by 0.21 mm. to about 0.95 mm. by 0.53 mm.

Third Instar.—Nine pairs of open spiracles occur in segments 2 to 10 inclusive (fig. 11, B), there being only 10 body segments during the early part of

the instar instead of the usual 13. The posterior spiracles of the previous instars are retained as the present ninth pair. As the larval feeding period terminates, a small buttonlike projection appears on the posterior surface of segment 10. It steadily increases until shortly before the meconium is cast. The transverse, slitlike anus is situated on the true segment 11, and segment 10 becomes incomplete ventrally and wedged between segments 9 and 11. This procedure was repeatedly observed with individual larvae maintained within glass cells.

The oral region is well-defined dorsally by means of a curved shelflike projection beneath which lies an elongate rounded sunken area. Four minute papillae occur just below each mandible; the oral aperture is situated directly under the dorsal projection.

The host, which has now spun its cocoon, never advances beyond the prepupa. Death is coincidental with the beginning of the last parasite instar—the destructive feeding period. Parasitized hosts remain active and seemingly normal until within several hours of this critical period. Occasionally the *Chrysopa* is killed before the cocoon is formed. In such instances parasite development proceeds as usual, the adults issuing from the chrysopid larval remains.

Where only one or two larvae occur per host, they may feed for a time before causing its death. Larval development is then slower than average, and the adults produced are larger than the average. When more than the usual number of larvae are present, development is speeded and the issuing adults are smaller. Thus both adult size and rate of development depend largely upon the number of inhabitants per host.

Very soon after the *Chrysopa* is killed, numerous swellings which rapidly increase in size appear just beneath the derm. An appearance similar to that produced by polyembryonic species often results. The presence of these dark brown, thin-walled compartments is always indicative of parasitism by *Isodromus.*

The larval membrane or sheath which appeared in the second instar is, at first, the same in appearance. If partially removed in normal salt solution, the smooth, glistening larval epidermis is seen to be nonwettable, as if thinly coated with oil. The sheath, however, has an affinity for water or similar liquids, and is thoroughly wettable. As the parasite larva becomes full fed the sheath stretches to its maximum dimensions, where it adheres to the host derm and commences to harden. Its incorporation with the host derm becomes so complete that the two are henceforth separately indistinguishable. The enclosed larva soon voids the meconium and decreases somewhat in size, leaving the now rigid covering as a loose-fitting shroud. Each larva is similarly encapsulated within its own compartment.

The origin of this sheath was not determined. Since it obviously differs from the larval integument, it could not be the previous exuvia. Sections were cut of ensheathed *Isodromus* larvae and pupae, but no additional information was obtained. No tracheal or other connections were found; it first appears as a very thin, closely enveloping membrane incomplete at the anterior end, later

forming an entire envelope which thickens and exhibits pigmentation. Thorpe (1936) has attributed sheath formation to a combination of phagocytic activity and host tracheal proliferation, whereas Flanders (1938) states that the labial and ileac glands secrete cocoon-forming substances in the Chalcidoidea. Whatever its origin, it is probably much the same in all species which exhibit similar structures. Sheath formation is apparently able to proceed with equal facility in those species which fully devour the host contents, as well as in those which complete development in the living host.

In those species which pupate within the still living host, the sheath is obviously a respiratory adaptation. With *Isodromus*, however, in which there are no definite tracheal attachments, its function is less clear. It may serve to protect the open spiracles of the last-instar larva while still immersed in the host fluids. The membrane would then allow interchange of oxygen and carbon dioxide.

The mandibles (fig. 11, A) are now heavily chitinized, and, except for the basal portion, are dark brown in color. They average 0.059 mm. in length.

The third instar occupies 7 to 13 days, the average about 8 days; and the prepupal period lasts 2 to 3½ days. The body contents of the host are entirely consumed within 1 to 2 days after death. Mature larvae vary greatly in size, according to the number per host. The average gain, however, is from 1.00 mm. by 0.53 mm. to approximately 2.40 mm. by 1.15 mm.

Pupa.—Pupation occurs 14 to 25 days after oviposition. The pupal stage averages about 11 days; the average pupa (fig. 11, C) measures 2.20 mm. by 0.90 mm. They lie grouped about the black host meconium, each within its own compartment, and surrounded by yellowish to brownish, flattened meconial pellets.

After remaining as adults within the *Chrysopa* cocoon for nearly 24 hours, during which time a portion of the ovarian eggs become mature, emergence is effected through holes gnawed in the host cocoon. Ordinarily there is but one exit hole per cocoon, although occasionally two or more occur. Emergence is most frequently at or near either end.

Number per Host and Sex Ratio.—From 345 field-collected cocoons, a total of 1,534 parasites issued for an average of 4.4 *I. niger* per host. Seventeen cocoons produced only 1 parasite apiece, whereas 10 parasites emerged from 3 cocoons. A maximum of 16 adults has issued from a single *C. majuscula* cocoon parasitized in the laboratory.

Of the 1,534 parasites recorded, 676 were females and 230 males, for a ratio of 2.9 females to 1 male. The majority of cocoons produced 2 to 4 females and only 1 male, but if there were more than 4 or 5 individuals, generally 2 or more males appeared in the approximate ratio of 3:1. Since *I. niger* is arrhenotokous, the occasional predominance of males is possibly due to duplicate ovipositions by both mated and unmated females.

Superparasitism.—One or more females may oviposit repeatedly in the same *Chrysopa* larva. Consequently, oviposition is frequently far in excess of the number which can possibly mature. In such instances development proceeds normally, though somewhat more rapidly, until the third instar. Death through

starvation soon intervenes, none of the larvae attaining maturity. When few supernumerary larvae are present, however, those individuals which first commence the final instar stage will speedily consume the host contents and mature while the others die of starvation. A very slight advantage of only several hours is often sufficient to determine the survivors.

Dissections of host cocoons will sometimes yield dead, undersized *I. niger* adults in all stages, from partial pupal eclosion to adults which have died while making exit holes. More than the average number of individuals are generally present in such cases. Here larval and pupal development was completed, but insufficient nourishment had prevented normal emergence. Evidences of superparasitism are relatively rare in the field under ordinary conditions, but when parasitism is high the percentage of "blanks" (*Chrysopa* cocoons which produce neither hosts nor parasites) increases.

Life Cycle.—In the following tabulation the "average" column approximates conditions during late spring, early summer, and most of autumn.

Life cycle	Extremes	Averages
	days	*days*
Egg	2.5– 4.0...	2.75
First instar	1.0– 1.5...	1.25
Second instar	2.0– 3.0...	2.25
Third instar	7.0–13.0...	8.0
Prepupa	2.0– 3.5...	2.75
Pupa	10.0–20.0...	11.0
Total	24.5–45.0	28.0

I. niger winters as pupae within the cocoons of *C. majuscula*. Approximately six months, from November to April, are passed in this stage.

Isodromus iceryae How.

I. iceryae was described in 1886 supposedly as a parasite of the cottony-cushion scale, *Iceryae purchasi* Mask. (Howard, 1886). It was later found, however, that the parasitized *Chrysopa* larva had cocooned within the hollow shell of the dead scale. All members of the genus *Isodromus* are parasites of the Chrysopidae. Since the description of the type, *I. iceryae*, six additional species have been recorded (Timberlake, 1919). Four of the seven are represented in this country.

Howard (1891) is of the opinion that the "*Aphelinus*" reared by Glover (1877) from *Chrysopa* in Maryland, was in reality *Isodromus*. The latter record would then constitute the first for the genus.

I. iceryae is listed from California, South Carolina, Kansas, Florida, Missouri, Maryland, and Washington, D.C., as well as from Mexico. The host list includes *Chrysopa californica* Coq., *C. rufilabris* Burm., and *C. lateralis* Guer.; several hemerobiids also on record must be regarded as questionable.

Girault (1917) described *I. abnormicornis* from Brazil, but Timberlake (1919) placed it in a new genus, *Brethesia*, adding a new South American spe-

cies, *B. latifrons*. Timb. Although no host records are available for *Brethesia*, it is likely that members of the genus will also prove to be parasites of *Chrysopa*. Two recent species of Girault's, *I. pulcher* and *Parataneostigma nigriaxillae*, are considered to be color variations of *I. iceryae*. I have reared both typical *pulcher* and *iceryae* individuals from the same cocoons, with specimens exhibiting intermediate color phases.

The morphology and biology of *I. iceryae* differs in several important respects from that of *I. niger*. The following account will therefore be primarily comparative in nature.
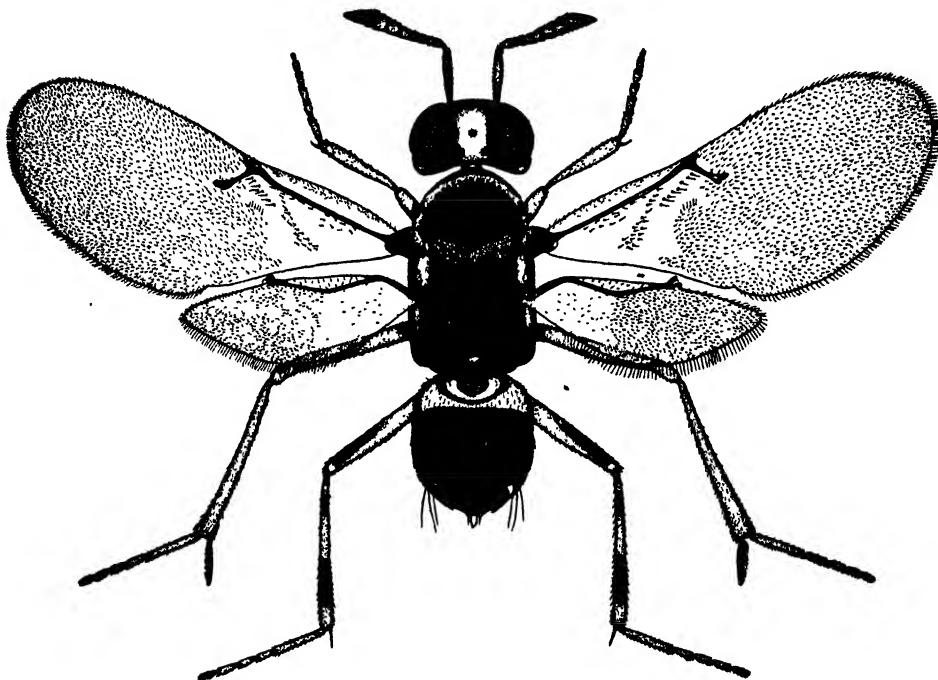
Fig. 12. *Isodromus iceryae* How. Adult female.

The Adult.—The female (fig. 12) is at once distinguishable from other *Chrysopa* parasites by its striking yellow and black coloration; the male is similar except for the smaller, more ovate abdomen; the black spots on the female venter are also almost absent in the male. *I. iceryae* is somewhat smaller than *niger*.

I. iceryae is noticeably more active than *niger*. When the sexes meet, a rather lengthy "introduction" ensues in which the parasites face one another with rapidly vibrating antennae as they run sidewise, often, in this manner, encircling the vial several times. This peculiar behavior is less pronounced with *I. niger*.

Host Specificity.—*C. californica*, the most abundant chrysopid in southern California, is the normal host of *I. iceryae*. It was never reared from *C. majuscula*, nor could oviposition be obtained under any circumstances. In the labora-

tory, larvae of *Eremochrysa punctinervis* (McLach.) were readily attacked and adults issued from the cocoons.

Of the valid host species in the literature, *C. rufilabris* and *C. californica* are closely related with respect to both larvae (Smith, 1922) and adults (Smith, 1932). *C. lateralis* and *E. punctinervis* are trash carriers. All four species are distinct from those of the "*nigricornis* section" to which *C. majuscula* belongs.

Oviposition.—The method by which several eggs are deposited simultaneously was observed in *I. iceryae*. In attempting oviposition, a female failed to insert the ovipositor properly, the eggs being extruded outside the host. Three of them appeared in rapid succession like tiny balloons, followed by a portion of the stalks. As the female moved away the egg cluster remained dan-
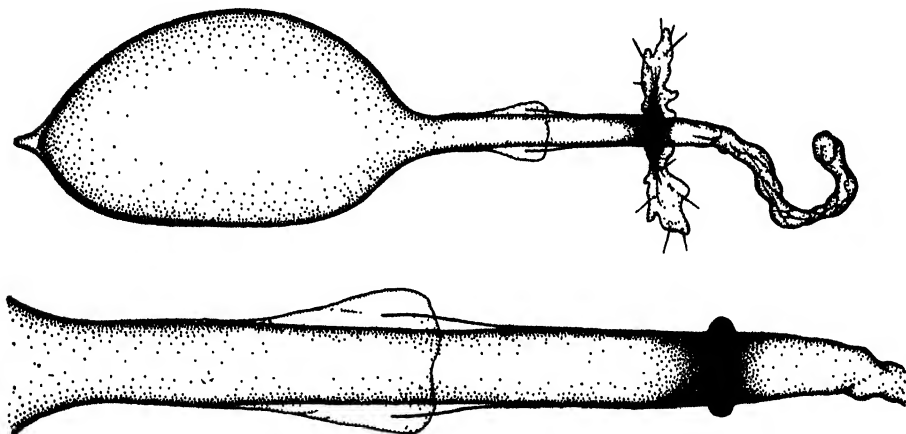
Fig. 13. *Isodromus iceryae* How. Deposited egg, lateral aspect, with eggstalk greatly enlarged.

gling until finally dislodged by the legs. Since the stalks lie parallel and tightly compressed within the ovipositor, its sudden withdrawal would leave them firmly wedged in the puncture, their tips projecting to the outside.

From 1 to 6 eggs are laid at a single insertion of the ovipositor, and, as in *I. niger*, repeated ovipositions may occur. The average number of eggs per cluster, however, was 3. The reproductive capacity of *iceryae* is approximately the same as that given for *niger*.

Egg: ovarian egg.—A transparent cone-shaped projection occurs on the distal end of the egg body in both the ovarian and deposited egg (fig. 13). The bulb is similar to that of *I. niger*, and average dimensions are the same except that the neck measures 0.14 mm. in length.

When eggs are dissected from mature females which have been dead for a short time, that portion of the neck which later contacts the host derm has become melanized, just as occurs in normally deposited eggs (fig. 13). This melanization is similar to that of the respiratory plate of *I. niger* under the same circumstances. It seems evident that the cellular structure of that portion is in some way distinct from the surrounding area. The "collar" is described below.

Deposited Egg.—Following deposition the bulb shrivels and hardens, forming a twisted threadlike strand which projects from the host. At this point the exuding fluids soon harden into a black ring. Each stalk is thus solidly attached to the adjacent one at the point of insertion.

Eclosion generally occurs 2½ to 3½ days from oviposition.

Comparative Morphology.—The absence of a respiratory plate in *I. iceryae* is most interesting from a comparative standpoint. Instead, a delicate, trans-
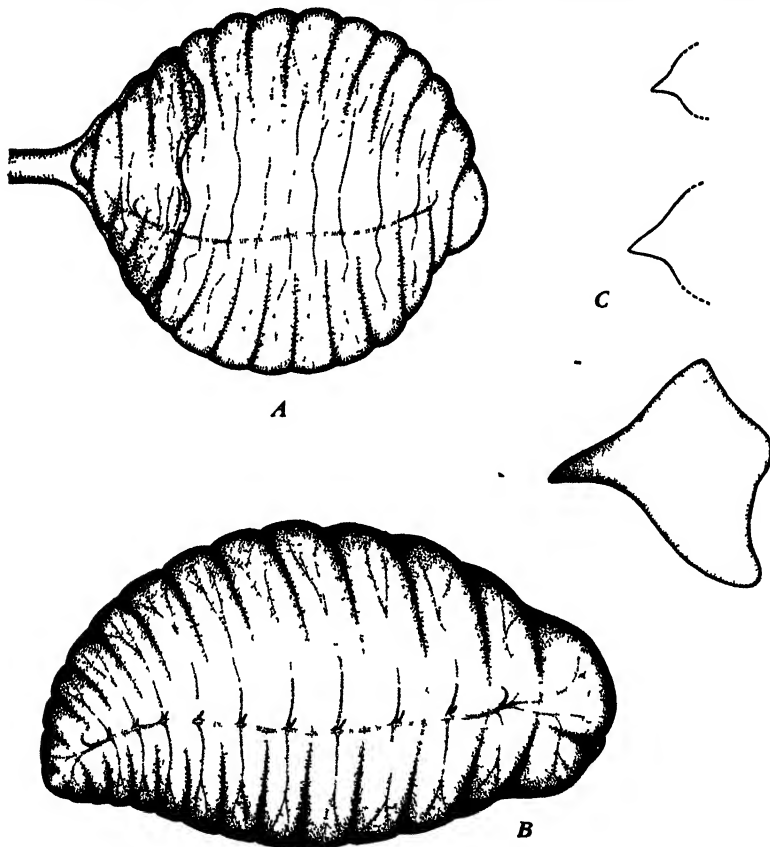
Fig. 14. *Isodromus iceryae* How. A. First instar larva showing caudal attachment. B. Second-instar larva. C. Larval mandibles, first, second, and third instars.

parent, membranous "collar" encloses the central portion of the stalk. Extending into the open end of the collar are a pair of rather definite lines which terminate abruptly; they may constitute a sort of secondary collar. The significance of this structure is exceedingly vague. It seems to be without function.

An interesting comparison is thus afforded between two species of the same genus with congeneric hosts. Although similar in general morphology and habit, the first two instars of *I. niger* are metapneustic whereas those of *I. iceryae* are apneustic. The presence of a respiratory plate in the former species but not in the latter would seem to furnish valuable circumstantial evidence concerning its function.

Larvae: first instar.—The spherical primary larva remains attached to the eggstalk by means of the persistent chorion which enfolds the posterior region (fig. 14, A). This attachment, however, is weaker than in *I. niger*. Great care must be exercised in dissecting the host or the larvae may become disengaged.

Segmentation is distinct; there are 13 body segments in addition to the head.
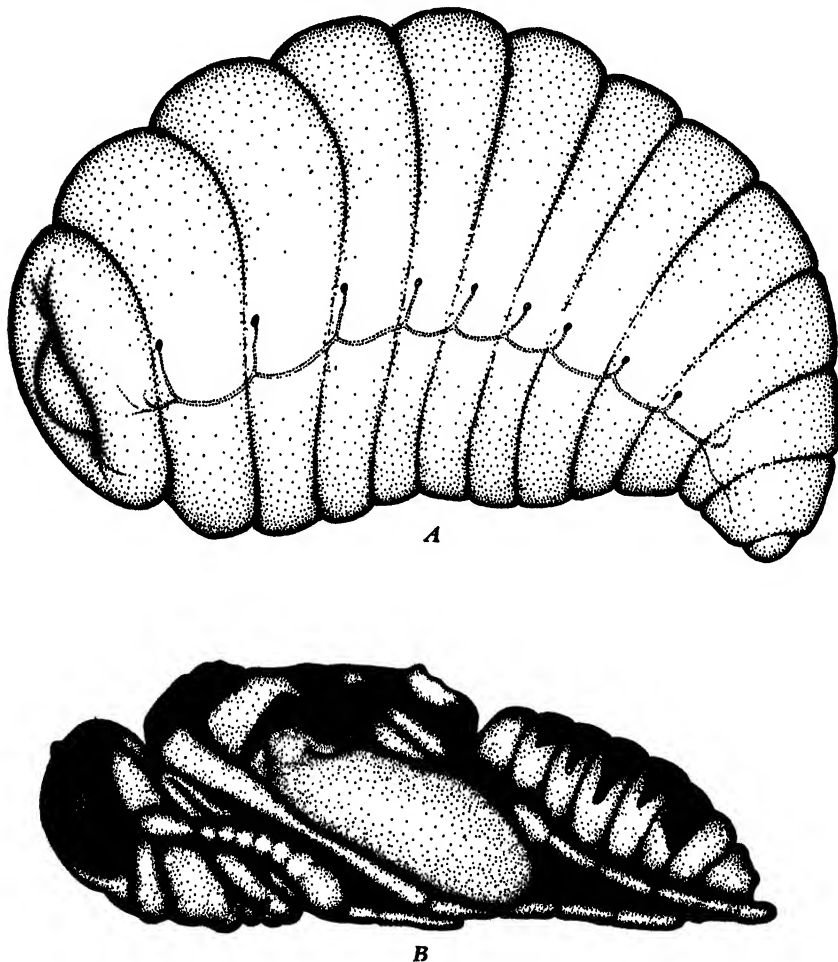
Fig. 15. *Isodromus iceryae* How. A. Mature third-instar larva. B. Mature pupa.

The respiratory system is apneustic, and there are 9 pairs of lateral tracheae (8 in *I. niger*). Apparently *iceryae* has evolved from the metapneustic to the apneustic type, retaining the caudal attachment after the eggstalk had lost its respiratory function.

The mandibles, when they can be distinguished, are also identical in both species (fig. 14, C). The points measure 0.004 mm. in length.

At ecdysis the molt skin is similarly retained at the edge of the chorion. The initial instar requires ¾ to 1½ days for its completion; average increment was approximately the same as that for *I. niger*.

Second Instar.—The larva has become considerably more elongate and the cephalic region is now well defined (fig. 14, B). The caudal attachment is maintained apparently during the entire instar, although only an occasional individual is successfully teased out still attached. Some of the larvae may break free within the host before the instar is terminated.

The tracheal system is still apneustic; paired spiracular spurs extend dorsally from the lateral trunks in segments 2 to 10 inclusive. A ninth pair is added in *iceryae* which lacks the posterior spiracles.

Both the first and second instars of *I. iceryae* are passed rather more rapidly than with *I. niger*. This is particularly noticeable in the second instar of *iceryae* which requires only ¾ to 1½ days for its completion (2 to 3 days in *niger*).

Third Instar.—The most obvious morphological divergence is in the larval segmentation. *I. iceryae* (fig. 15, A) has 13 body segments whereas *niger* has only 11. The ninth pair of spiracles are thus situated on the penultimate segment of the latter species, whereas there are three segments caudad to the final pair in *I. iceryae*. A larval membrane or sheath also occurs in *iceryae*.

Third-instar larvae increase from approximately 0.90 mm. by 0.50 mm. to about 2.15 mm. by 1.05 mm.

Pupa.—The pupa (fig. 15, B) is first observed 10 to 19 days following oviposition, the average being 13 days. Duration of the pupal stage averages 9 days (11 days in *I. niger*). Pupal dimensions are approximately 2.00 mm. by 0.86 mm.

Of 100 previously parasitized cocoons, 79 contained a single exit hole, 20 had two exit holes apiece, and 1 cocoon was pierced by three separate holes.

Number per Host and Sex Ratio.—From 1,523 field-collected cocoons parasitized by *I. iceryae*, there emerged 3,545 adults for an average of 2.3 per host. Three hundred and fifty-six or 23.3 per cent of the cocoons produced only 1 parasite each, whereas 6 *iceryae* emerged from 4 cocoons, and a maximum of 7 parasites issued from a single host cocoon. In laboratory experiments no more than 9 *I. iceryae* adults per host could be reared.

The sex ratio was approximately 2 : 1, with females predominating. Because of the fewer parasites per host in *iceryae*, the ratio is more nearly equal which insures the presence of both sexes in the majority of cocoons.

Parthenogenetic reproduction in *I. iceryae* is arrhenotokous; superparasitism similar to that described for *I. niger* also occurs.

Life Cycle.—An outline of the life cycle follows.

Life cycle	Extremes	Averages
	days	*days*
Egg	2.5 – 4.0	3.0
First instar	0.75– 1.5	1.0
Second instar	0.75– 1.5	1.0
Third instar	5.0 – 9.0	6.0
Prepupa	1.0 – 3.0	2.0
Pupa	8.0 –15.0	9.0
Total	18.0 –34.0	22.0

The life cycle of *iceryae* averages approximately 6 days less than that of *niger*, although the incubation period is shorter in the latter species. During midsummer the third instar may be attained, and the host killed barely 4 days from oviposition. The body contents are entirely consumed by the end of the following day. Since the life cycle of *C. californica* is invariably shorter than that of *C. majuscula*, the two species of *Isodromus* appear well synchronized with their respective hosts.

I. iceryae also overwinters as pupae within the cocoons of its host.

Chrysopophagus compressicornis Ashm.

According to Ashmead (1894), whose *C. compressicornis* is the type species, the genus *Chrysopophagus* is very close to *Cheiloneurus*, a group predominantly hyperparasitic in habit.

C. compressicornis is recorded from South Carolina and Mississippi from the cocoons of *Chrysopa rufilabris* Burm. and *C. attenuata* Walk.; I have reared it as a hyperparasite of both *C. californica* and *C. majuscula*. McGregor (1914) also bred this species from an undetermined syrphid puparium. Six additional species have since appeared in the literature, none of them accompanied by host records.

Museum specimens have been examined, labeled "ex. mealybug on weed roots—secondary on *Chalcaspis*," and "ex. *Pseudococcobius* in *Eriococcus* on *Croton*," both from California. The species of *Cheiloneurus* are for the most part secondary parasites of various coccids, and *C. compressicornis* apparently shares this habit to a certain extent.

The Adult.—The female (fig. 16) is much larger than the male, being further distinguished by the prominent black compressed flagellum and by the tuft of black bristles on the scutellum. The body is distinctively patterned in orange yellow and black; the antennae are slender with numerous long setae in the male.

Mating occurs readily in the laboratory; the same male will pair repeatedly with different females.

Oviposition.—More than one egg is generally laid at a single insertion of the ovipositor, two or three being the usual number. With *I. iceryae*, which is the most common host, deposition is usually effected in each individual. Occasionally, however, one or more of them escape parasitization, so that both *Isodromus* and *Chrysopophagus* adults emerge from the same cocoon.

Following a rather deliberate antennal examination, the ovipositor is forced downward through the walls of the *Chrysopa* cocoon. A series of probing motions then ensues by which the parasite determines its suitability for oviposition. Upon contact with a free parasite individual, either primary or secondary in relation to the chrysopid, deposition occurs subcutaneously. Oviposition is never effected in parasitic individuals still surrounded by host fluids.

The chrysopid cocoon, which furnishes ordinarily the primary oviposition stimulus, is not essential. Eggs were deposited in *Isodromus* pupae enclosed within their sheaths, but separated from the *Chrysopa* cocoon. Similar results were secured when dead host larvae containing *Isodromus* pupae were offered.
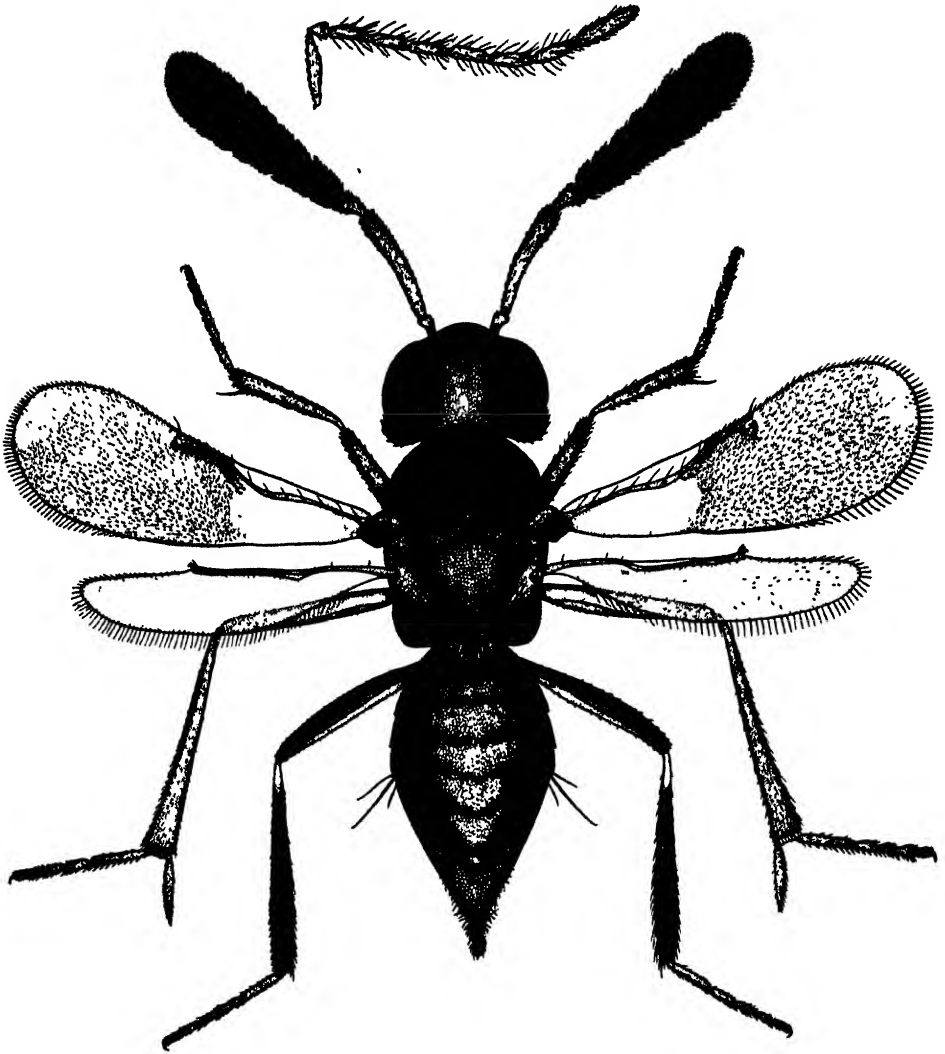
Fig. 16. *Chrysopophagus compressicornis* Ashm. Adult female and male antenna.

, After repeated attempts, several eggs were finally laid even in bare *I. niger* pupae.

Egg: ovarian egg.—The double-bodied ovarian egg (fig. 17, A) exhibits the following average measurements:

Length of egg body..............................0.16 mm.
Width of egg body............... ....0.06 mm.
Length of neck........................ ....0.22 mm.
Length of bulb..... .... 0.10 mm.
    Total length.... ....0.49 mm.

Deposited Egg.—After deposition the bulb decreases to an apical swelling on the tip of the stalk (fig. 17, B). At high magnifications, a tiny black dot is

often apparent on the chorion at the extreme tip; this is presumably the micropyle.

The egg is deposited free in the body fluids of its host; only occasionally, and apparently by chance, is the stalk partially embedded in host tissue. It soon commences to swell, at first gradually, then more rapidly. The following observations were made during December when the incubation period averaged 4 days.

The contents of the freshly deposited egg are uniformly whitish, but at the end of the first day the columnar blastoderm is found completely encircling the darker central portion or yolk (fig. 17 C). There is some evidence of cellular proliferation at the apical end, which may be involved in the formation of the embryonic membrane.

At 2 days (fig. 17, D), a slight increase in size was first noted, average dimensions being 0.20 mm. by 0.09 mm. The stomadeal invagination, following the ventral indentation of the embryo, is typical of this period. Since the embryology of *C. compressicornis* was not investigated, the origin of the embryonic membrane could not be determined; the more general term "trophic membrane" is therefore adopted. The membrane first appears completely encircling the embryo between 1 and 2 days after oviposition, coincident with the initial swelling of the egg. Embryonic growth thus begins through absorption of host fluids. Trophic membranes of this type occur in various families; the papers of Jackson (1928) and Vance (1931) present comparative summaries.

Figure 17, E, shows the egg at 3 days, or approximately 1 day prior to eclosion. Average measurements are 0.43 mm. by 0.19 mm. Here the embryo exhibits a great advance over the previous day. Bodily form is distinct, although no trace of segmentation is yet apparent, and the eggstalk has begun to degenerate. The cephalic end of the embryo is invariably the stalked end. Jackson (1928) and others have found the petiolate end always caudal in certain species, whereas the reverse is true in several other instances.

In many species the embryo is surrounded by a fluid-filled space which separates it from the trophic membrane. In *C. compressicornis*, however, the membrane is a tightly fitting envelope which stretches with embryonic growth. The transparent chorion has become greatly attenuated and is easily ruptured. The trophic membrane is well defined; cell walls are nearly always indistinguishable, however, even in stained preparations, although the prominent oval nuclei are invariably distinct. They average 0.044 mm. in diameter.

On what is apparently the surface of the trophic membrane, between it and the chorion, numerous small vesicles similar to minute bubbles are seen. Although usually found scattered over the surface in an irregular manner, they occasionally become arranged in regular circles. Jackson (1928) has described a similar arrangement in *Dinocampus rutilus* Nees in which they are said to align themselves along the cell boundaries, thus obscuring them from view. Miss Jackson is of the opinion that they represent dissolved nutritive matter derived from the body fluids of the host.

On the fourth day, just before eclosion, the egg has increased to an average of 0.73 mm. by 0.27 mm. All that remains of the stalk is a rounded projection

on the cephalic end of the chorion. The mature embryo with the tail still bent beneath the body exhibits a restricted squirming motion. The trophic membrane is unchanged except that the cells have become considerably attenuated. Although greatly increasing in size, the egg still retains its original proportions.

From oviposition to eclosion the egg increases approximately 4½ times in length and breadth. Although this is somewhat less than the increase occurring in *Dinocampus*, it is exceeded by *Tetracnemus pretiosus* Timb. (Clancy, 1934),
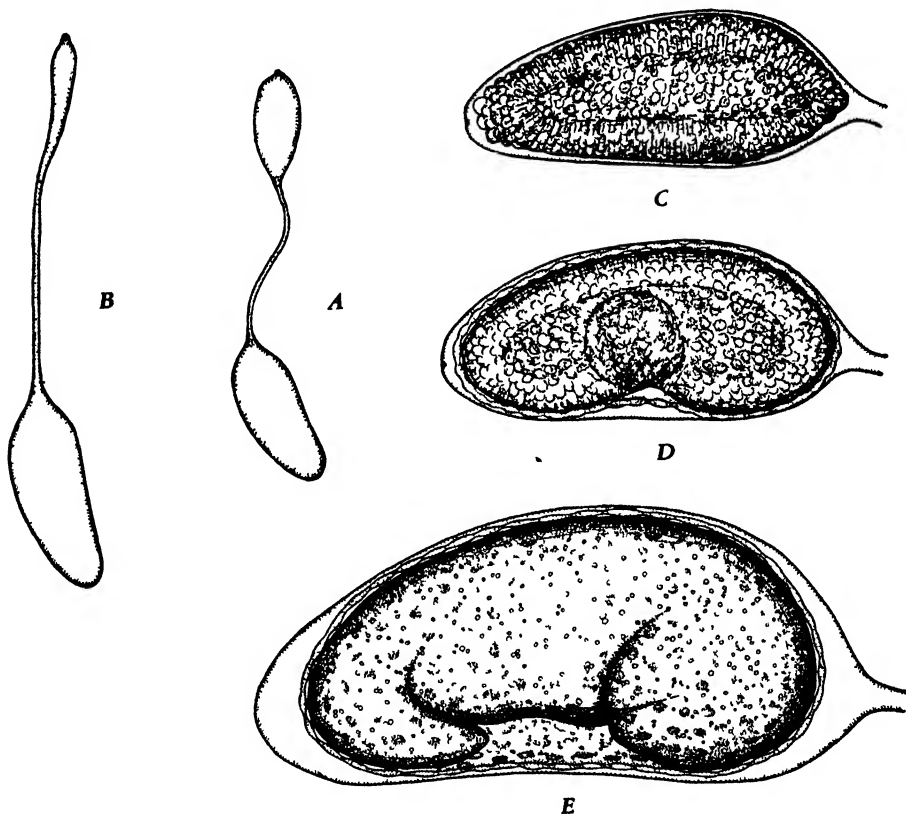
Fig. 17. *Chrysopophagus compressicornis* Ashm. A. Ovarian egg. B. Newly deposited egg. C. Egg, 24 hours. D. Egg, 48 hours. E. Egg, 72 hours.

which increases 6 to 8 times in length. Other encyrtids which exhibit this phenomenon are *Achrysopophagus modestus* Timb., the egg of which increases 2½ times in length (Clausen, 1924), and that of *Cheiloneurus noxius* Comp., which increases 4 times in length (Le Pelley, 1937). Compere and Flanders (1934) illustrate the eggs of *Anarhopus sydneyensis* Timb.; an increment of approximately 4 to 4½ times is indicated. None of the investigated petiolate encyrtid eggs, which are suspended within the host, "banded" or otherwise, exhibit this characteristic. Only those which are free of attachment have been shown to increase perceptibly in size.

Larvae: first instar.—Eclosion is probably effected by the larva straightening out within the egg, the pressure thus exerted rupturing the chorion at either

end. Immediately afterward the trophic membrane is found encircling the mid-region; the head and tail protrude at either end (fig. 18, A). The chorion has been sloughed off and has disappeared. In *Dinocampus rutilus* the ruptured
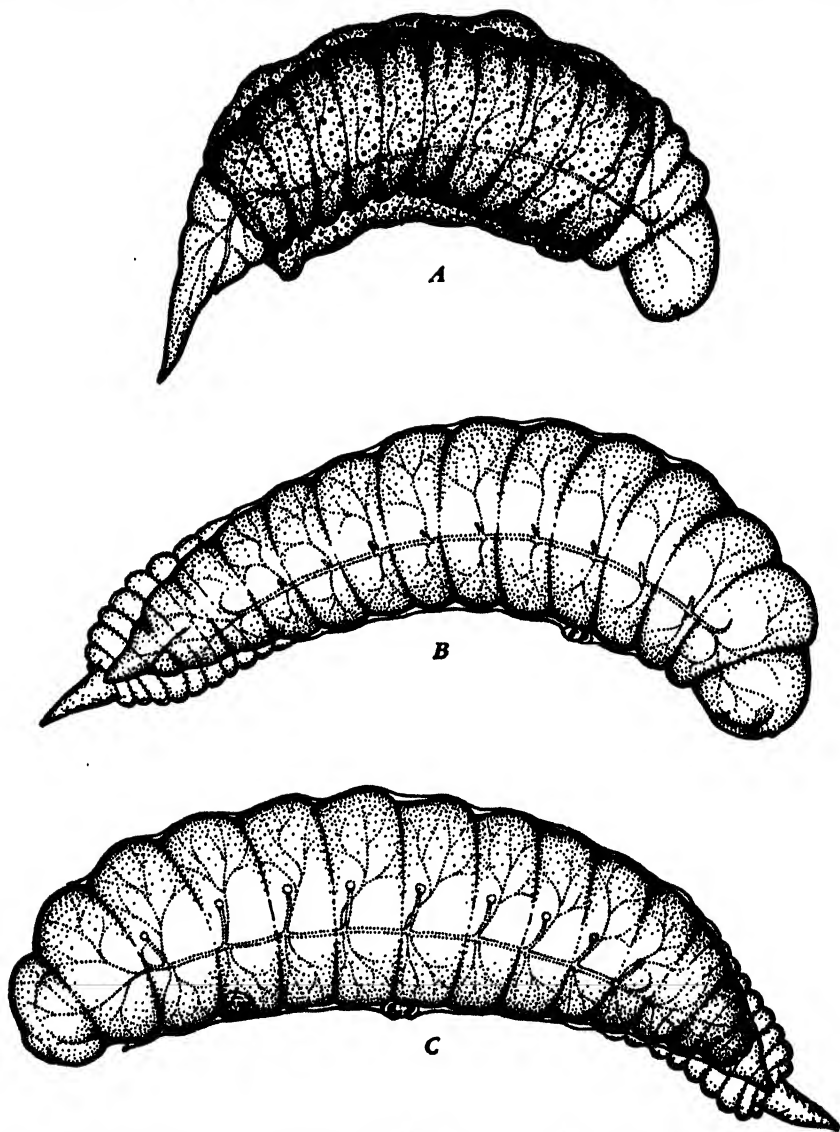
Fig. 18. *Chryeopophagus compressicornis* Ashm. A. First-instar larva showing trophic membrane. B. Second-instar larva showing persistent larval exuvia. C. Third-instar larva prior to leaving host, showing persistent larval exuviae.

chorion remains surrounding the trophic membrane throughout at least the first instar. The peculiar dissociation and subsequent growth of the cells of the embryonic membrane as noted in *Dinocampus* and others is entirely lacking in *C. compressicornis*. The trophic membrane remains unchanged throughout the instar, becoming tight fitting as the larva increases in size.

The newly emerged primary larva is characterized by a prominent, pointed tail as in the recorded species of *Cheiloneurus* and related genera. The head is well defined with the mouth·directed anterioventrally; there are 12 body segments exclusive of the caudal prolongation, segments 2 to 7 inclusive being divided dorsally into two equal subsegments. These constrictions disappear as the larva becomes distended with food.

Tracheation is of the usual apneustic type; there are nine pairs of lateral branches extending dorsally and ventrally in segments 2 to 10 inclusive.

The mandibles (fig. 19, A) are well defined with heavily chitinized points, and average 0.033 mm. in length. An increase from 0.74 mm. by 0.23 mm. to 0.90 mm. by 0.28 mm. was made in the ¾ to 1½ days spent as primary larvae.

Second Instar.—The entire second instar is passed within the exuvia of the primary larva, except that the head and first two segments protrude anteriorly (fig. 18, B). Fragments of the trophic membrane frequently adhere to the exterior, and in some instances it apparently persists in a more or less tattered condition throughout the instar.

In general appearance, the first two instar larvae are much alike except that the tail has undergone great reduction; a short, conical projection is all that remains. The addition of nine pairs of blind spiracular spurs in segments 2 to 10 is also characteristic.

The mandibles measure 0.030 mm. in length, being smaller and less heavily chitinized than in the primary larva (fig. 19, B). The time required for the second instar is ¾ to 1½ days. The larva increases in size from 0.90 mm. by 0.28 mm. to approximately 1.10 mm. by 0.33 mm.

Third Instar.—Death of the host is generally coincident with the beginning of the third and final instar. The first- and second-stage exuviae are found enclosing all but the extreme anterior region of the newly molted larva (fig. 18, C). Both sets of mandibles may be distinguished ventrally.

The larva is now entirely noncaudate, consisting of a less prominent head and 13 segments. The anus has changed from ventral to terminal position. Nine pairs of open spiracles are present, and the persistent larval skins serve to exclude the host fluids. Immediately prior to ecdysis the completed spiracular structure is faintly discernible in glycerine mounts; at the molt, the entire structure fills with air and presumably functions by diffusion through the enveloping larval skins.

Within 24 hours the hyperparasite larvae emerge through apertures cut in the body wall, freeing themselves of the accumulated larval exuviae which remain plugged in the orifices just vacated. The larvae then feed externally until all nourishment is subtracted, leaving only the crumpled host skin. Respiration is now holopneustic, the spiracles being free to operate in the manner of ecto-parasitic larvae.

Owing to the variable number of parasitic inhabitants, individual size varies greatly. Average increment, however, was 1.10 mm. by 0.33 mm. to 1.60 mm. by 0.58 mm. The mandibles, which also varied accordingly, averaged 0.046 mm. in length. Depending upon the temperature, 3 to 9 days are spent as third-instar larvae.
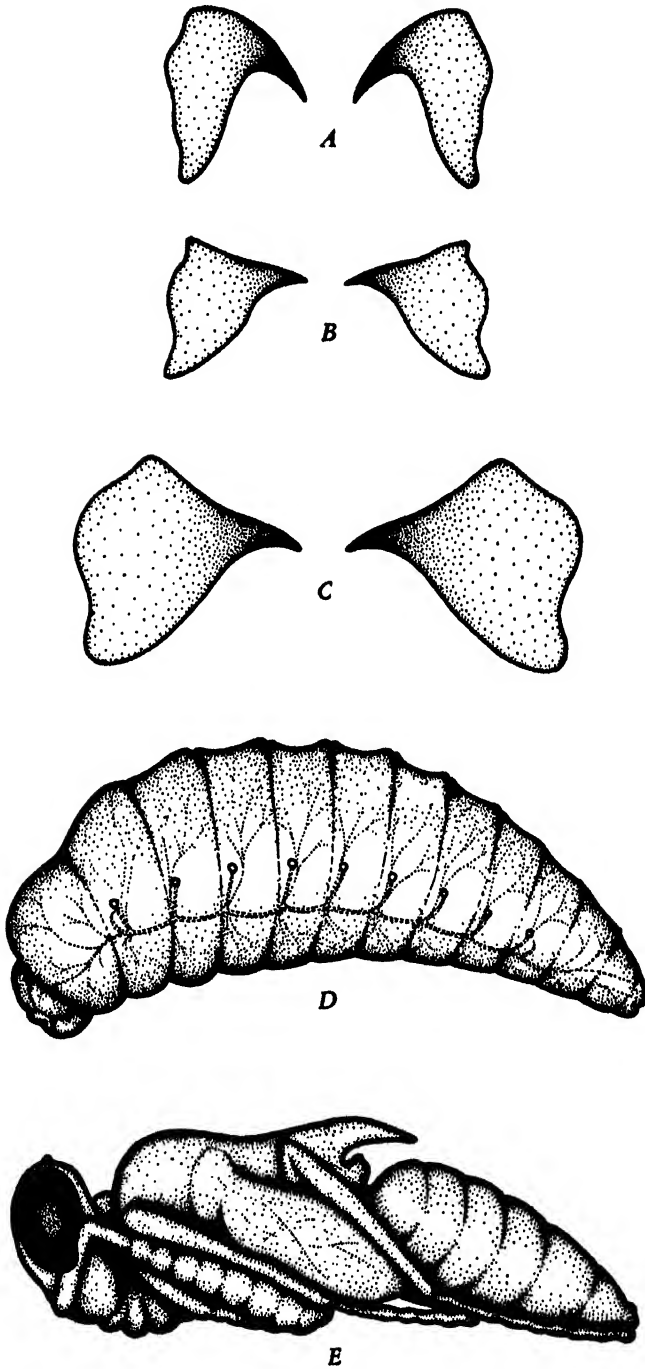
Fig. 19. *Chrysopophagus compressicornis* Ashm. A. First-instar mandibles. B. Second-instar mandibles. C. Third-instar mandibles. D. Mature third-instar larva after leaving host. E. Female pupa.

Pupa.—Pupation occurs 8 to 19 days after oviposition, with an average of 10 days; approximately 7½ days are passed as pupae. *C. compressicornis* overwinters in the pupal stage.

The female pupa (fig. 19, E) is readily distinguishable by means of the pointed thoracic projection which encloses the scutellar bristles. Male pupae average 1.26 mm. by 0.50 mm., whereas the larger female pupae approximate 1.75 mm. by 0.66 mm.

Upon emergence the adults issue from the *Chrysopa* cocoon through tiny exit holes cut in the walls. The number and position of these holes vary, but their extremely small size distinguishes them from all others except those made by *Tetrastichus*.

Number per Host and Sex Ratio.—Of 218 field-collected *Chrysopa* cocoons from which *C. compressicornis* emerged, there were 1,113 parasites for an average of 5.1 per cocoon. Seventeen cocoons produced only 1 parasite each, and 10 or more individuals were reared from 14 cocoons. The maximum number, 13 *Chrysopophagus*, emerged from only two cocoons. In laboratory rearings a maximum of 16 parasites was secured. *C. compressicornis* is only occasionally hyperparasitic on *Chrysopa majuscula;* 5 of the 218 cocoons were of that species, *Isodromus niger* being the primary host in each case. Because of the larger size of *C. majuscula*, an average of 7.4 hyperparasites developed per host cocoon.

The sex ratio, as calculated from the above material, was 3.1 females : 1 male. Parthenogenetic reproduction is always arrhenotokous; those rearings which resulted in entirely male progeny (6 in number) were probably due to oviposition by unmated females.

Superparasitism.—When large numbers of ovipositing females are provided with too few hosts, egg deposition occurs repeatedly and at random. As many as 40 eggs were found within a single *Perilampus chrysopae* pupa subjected to excessive parasitization. In another instance 24 individuals pupated—with several *I. iceryae* as hosts—but only 15 pupae produced adults. Again, 14 first- and second-instar larvae were dissected from a single *I. iceryae* pupa which was already dead and the body fluids largely consumed. Such examples of superparasitism can result only in the death of both hosts and parasites.

Emergence from Adult Host.—When oviposition occurs in mature host pupae, normal development ensues and the full-grown larvae issue from the adult host. This unusual phenomenon was observed repeatedly in laboratory-parasitized individuals. It is essential, however, that oviposition be effected in host pupae which will emerge within approximately 24 hours. The larvae are nearly always found in the abdomen where body fluids and softer tissues are most abundant. Soon after attaining the third instar (the adult host having been killed), the larvae emerge from the anus or through the softer intersegmental areas of the abdomen, forcing the adjacent sclerites sharply outward at the point of issuance. The host adult may remain active and apparently normal for several days prior to larval emergence. It would be of interest to ascertain whether physiological castration is induced by the parasite in such instances.

C. compressicornis larvae have issued from the adults of *Isodromus niger*, *I. iceryae*, *Perilampus chrysopae*, and *Hemiteles tenellus*. Berry (1938) has also reared *Tetrastichus brevistigma* Gahan from adults of the elm leaf beetle.

Life Cycle.—Under laboratory conditions the life cycle is as follows:

Life cycle	Extremes	Averages
	days	*days*
Egg	2.5 – 4.5..	3.0
First instar	0.75– 1.5..	1.0
Second instar	0.75– 1.5..	1.0
Third instar	3.0 – 9.0..	3.5
Prepupa	1.0 – 2.5..	1.0
Pupa	5.0 –14.0..	7.5
Total	13.0 –33.0..	17.0

PERILAMPIDAE

Perilampus chrysopae Cwfd.

The original description of *P. chrysopae* (Crawford, 1914) was made from specimens reared from the cocoons of *Chrysopa* sp. in South Carolina. Crawford later (1916) designated the color variety *laevicephalus* from California specimens, *Chrysopa californica* being the host. Both forms were encountered during the present study.

Subsequent records indicate a very general distribution. Smulyan (1936) disregards the variety *laevicephalus*, recording the species from thirty-one states throughout the United States, and also from Canada. Specific host records are lacking in nearly all instances.

In addition to *C. californica*, specimens have been reared from *C. rufilabris* Burm. Smith (1922) records *Perilampus* sp. (undoubtedly *P. chrysopae*) questionably from *C. oculata* Say. Ashmead's (1895) reference to *P. hyalinus* Say from the cocoon of *C. attenuata* Walk. was probably *P. chrysopae*. Essig (1926) mentions *Sympherobius angustus* (Banks) and related species as hosts of *chrysopae*, although I was unable to corroborate this observation.

The species of *Perilampus* seem to be largely hyperparasitic, although the true host relationships are definitely known in only a few instances. Primary parasitism has been demonstrated only in *P. chrysopae* and *P. italicus*. Further biological information on the Perilampidae is furnished by Bergold and Ripper (1937), who have added to Parker's account (1924) of *P. tristis* Mayr. Martelli (1932) also gives a brief account of *P. italicus* as a primary ectoparasite of the tenthredinid, *Athalia colibri* Christ.

H. S. Smith (1912) was first to discover the remarkable hypermetamorphic development within the Perilampidae in *P. hyalinus*, later (1917) demonstrating the habit of leaf oviposition in *P. chrysopae*. Wheeler (1907) had previously described a planidium larva in the closely related family Eucharidae; more recently Clausen (1928) and others have shown indirect oviposition to be characteristic. Clausen (1929) has added the Trigonalidae to the list of families exhibiting indirect oviposition and planidium-type larvae.

The Adult.—The stocky, compact body and coarsely punctate thorax serves immediately to distinguish *Perilampus* from all other *Chrysopa* parasites. The adults (fig. 20) are unusually lethargic, in sharp contrast to the other species. Under crowded conditions they will attack one another with their powerful mandibles, severing legs and antennae and causing premature mortality. Single adults in separate vials lived 20 to 58 days. Martelli (1932) has recorded the same behavior in *P. italicus*.

Oviposition.—Oviposition was readily secured by enclosing aphid-infested leaves within glass or celluloid cylinders exposed to strong light. The petioles
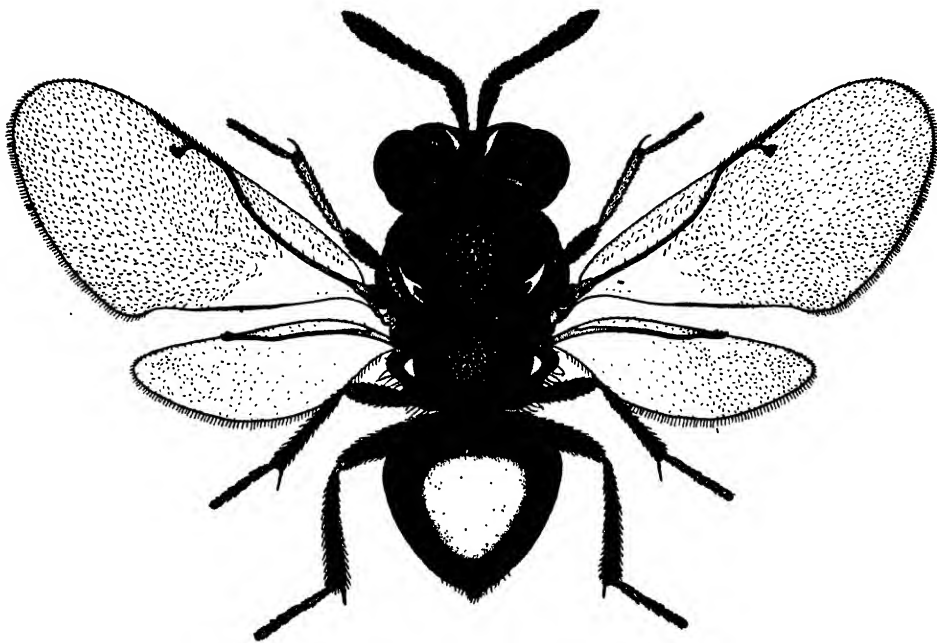
Fig. 20. *Perilampus chrysopae* Cwfd. Adult female.

were placed in cotton-stoppered water bottles, and honey solution was streaked on the leaves daily. An infusion of crushed aphis was found to give equally good results, and mealybugs, either living or crushed, also sufficed. When mature females were kept for some time before being allowed to oviposit, their eggs were deposited upon bare leaves and occasionally even within empty glass vials. Under such conditions, however, oviposition is greatly reduced. Few eggs were deposited in subdued light.

Most of the eggs were placed on the undersides of leaves alongside and parallel with the midribs; of 176 eggs recorded as to position (laboratory oviposition), only 1 was on the upper surface, 129 were along the midrib, and the remaining 46 eggs were scattered over the ventral surface. The type of leaf— pubescence, prominence of veins, and so forth—influences egg location, since they are generally to be found in more protected places, rather than on smooth, exposed surfaces.

Oviposition is effected by briefly touching the tip of the abdomen to the leaf surface; the ovipositor is of the usual chalcidoid type, but it is very short. The preoviposition period varies from 3 to 11 days with different individuals. An unmated female laid 322 eggs in 45 days for an average of 7.4 eggs per day; a maximum of 46 eggs was laid in one day. Following a preoviposition period of 10 days, only 21 eggs were deposited during the first 9 days, whereas 70 eggs were laid during the last 9 days.

From various females which had been isolated for several weeks 40 to 93 mature ovarian eggs were dissected; the innumerable immature ova could not be accurately counted.

The normal reproductive capacity probably ranges from 200 to 500 eggs. Although somewhat in excess of the number deposited by most chalcidoids, it is far exceeded by the trigonalid *Poecilogonalos thwaitesii* (Westw.), which holds the record among the parasitic Hymenoptera of 10,641 eggs deposited by a single female (Clausen, 1929). As Smith (1912, p. 39) so aptly states: "insects which are subject to very high mortality in their younger stages must have a high potential rate of reproduction in order to offset this loss and still prevent the species from becoming extinct."

Egg: ovarian egg.—When fully mature the ovarian egg (fig. 21, A) measures 0.30 mm. by 0.08 mm. The surface is perfectly smooth, and one end is drawn out into a bluntly rounded projection.

Deposited Egg.—The deposited egg (fig. 21, B) is characterized by a series of minute ridges which connect to form numerous irregular cells on the surface of the chorion. It seems likely that the chorion is thus molded by contact with the uterine walls, either during or immediately before deposition.

The egg is milky white in color, and although lying exposed to the elements, it is nonsclerotized and extremely delicate. Average dimensions have altered slightly; the egg is now somewhat shorter and broader and the petiole is less pronounced. The blunt end is lightly attached by means of a sticky exudate to the leaf surface; it lies at a slight angle with the opposite end uppermost.

Depending upon the temperature, 4 to 12 days are required for incubation. Eggs laid during the summer months usually hatch in 4 to 6 days. Emergence occurs at the petiolate end.

Larvae.—Three larval instars have been distinguished as in *P. hyalinus* (Smith, 1912), although Parker (1924) found four instars in the same species. Bergold and Ripper (1937) have also described four larval instars in *P. tristis*.

Primary Larva.—The motile first-instar larva or planidium (fig. 21, C) consists of a well-defined head and 12 body segments, the sclerotized, dark brown segmental plates cover all but the narrow median ventral portion which is membranous. The body is capable of extreme distension and contraction. The oral region is also membranous and may be partially extruded; segment 12 bears a fleshy anal sucker which appears to be coated with a viscous secretion. The sucker is capable of extension to assist in locomotion, and of attachment to leaf surfaces. A single pair of spiracles is situated on the lateral margin between segments 1 and 2 in the intersegmental membrane; the armature no segment 1 is slightly notched to accommodate the spiracular apertures. No

ventral hooks could be distinguished, and the ventral margins of the segmental plates are relatively simple as compared with other perilampids. The trend toward a more simplified type is evident in the planidium of *P. chrysopae*.

Locomotion is effected by means of a looping movement similar to that of geometrid larvae, although soon after emergence the planidium attaches itself to the leaf surface by the anal sucker, the body standing at right angles to the leaf. In this position the planidium awaits its host. At the approach of any moving object it frantically reaches and twists about in an effort to attach itself, the vibrations of the leaf having forewarned the parasite of the approach of a possible host. When contact is made the planidium immediately takes firm hold with the mandibles and remains attached. Only those individuals
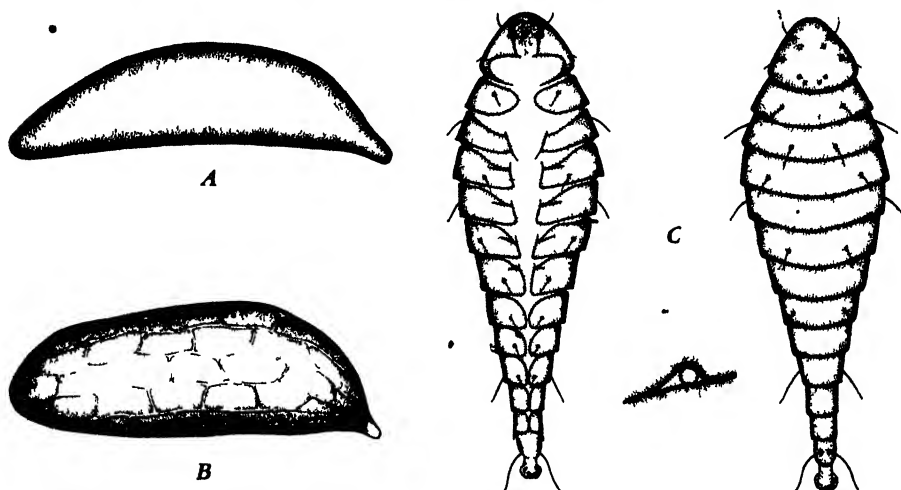
Fig. 21. *Perilampus chrysopae* Cwfd. A. Ovarian egg. B. Deposited egg. C. Dorsal and ventral aspect of newly emerged planidium showing enlarged spiracle.

which reach a *C. californica* larva are able to develop, the others eventually dying from starvation. Should its carrier die, however, the planidium disengages the mouth parts and again resumes its waiting attitude.

Although no nourishment is taken while awaiting the host, the planidia are remarkably long lived for such apparently delicate creatures. Smith (1917) has had them live for 17 days without changing position. Feeding is begun only after the host has pupated; even during the prepupal period no nourishment is apparently obtained, although the mouth parts are firmly embedded. In *P. hyalinus*, Smith found that the change from endoparasitism to ectoparasitism (the planidium feeding only as an ectoparasite) also coincided with host pupation, the actual stimulus being that of histolysis in the host larva. Although *P. chrysopae* is always ectoparasitic, the initial feeding stimulus is apparently the same. Planidia transferred to *Chrysopa* pupae, even though they be newly formed, never showed evidence of feeding, and the hosts invariably produced adults.

The *Chrysopa* pupa becomes inactivated either during the first or second parasite instar, and although the larva is immediately removed death occurs.

A condition similar to that produced by *Hemiteles tenellus* adults which fatally paralyze their hosts was noted. The parasitized individuals assumed a peculiar semitransparent, glassy aspect, and eventually died. Normal *Chrysopa* pupae are extremely active when stimulated, but those fed upon by *Perilampus* larvae became less responsive and were soon entirely motionless. The pulsating dorsal vessel or heart, which is always prominent in *Chrysopa*, was an excellent indicator of condition. Death could be definitely noted as pulsations ceased entirely.

As the host becomes motionless or "paralyzed," the heart pulsates more and more slowly. Generally within 24 hours the characteristic glassy aspect becomes apparent, increasing gradually in extent. The most noticeable feature is the gradual clearing or destruction of pigmentation in the compound eyes. The dorsal vessel contracts into a thin line which pulsates so weakly as to be barely perceptible. The pupa has meanwhile assumed a yellowish tinge which deepens to amber after death. Pupae from which *Perilampus* has been removed remained alive for as long as 7 days after paralysis was first noted. Paralyzed pupae also remained in a preserved condition (without decay or desiccation) much longer than pupae which had died from other causes.

Paralysis is probably induced through the injection of a specific larval secretion, and is undoubtedly twofold in purpose: it protects the delicate parasite larva from injury by an otherwise active host, and it ensures a continuous supply of available food. Smith believed that with *P. hyalinus* the peculiar glassy appearance assumed by the host was due to arrested histogenesis caused by the burrowing planidium, since it became evident even before the planidium commenced feeding. In *P. chrysopae*, however, which is solely ectophagus, this condition generally appears at about the time of the first larval molt, and sometimes not until midway in the second instar.

Although *P. chrysopae* will never develop on *C. majuscula*, a very puzzling relationship has been noted. In October a number of overwintering *majuscula* prepupae were isolated in glass cells, and a newly emerged *Perilampus* planidium was transferred to each one. Periodic inspections showed the planidia alive and firmly attached, although exhibiting no signs of having fed. Adult chrysopids emerged during March and April, the planidia being still alive and active. From five to six months thus elapsed, apparently without feeding, upon a host which is unsuitable for *Perilampus* development. A parallel case is provided by Clausen (1928), who found that the planidia of *Schizaspidia manipurensis* Clausen would overwinter upon *Camponotus* larvae which were unsuitable as hosts; approximately six months were also passed without evidence of feeding.

In dissecting field-collected *C. majuscula* cocoons, *Perilampus* planidia are frequently encountered on the prepupae or are found dead attached to the molt skins. With *C. californica*, those individuals are lost which fail to disengage themselves at the molt. Dead planidia are also commonly found attached to the inflated host remains typical of *Isodromus* parasitism.

The larvae may attach themselves at any point on the host derm, and a variable number of planidia occur upon a single host individual, although never more than one adult is produced per cocoon.

In an effort to determine whether *P. chrysopae* would develop hyperparasitically, planidia were placed upon a series of *Isodromus iceryae* and *I. niger* larvae and pupae in glass cells. Results were negative in every instance, and though the mandibles were attached in the usual fashion, there was no increase in size. One planidium remained alive upon an overwintering *I. niger* pupa for a total of 85 days.

As feeding commences, the intersegmental membranes and ventral portion become distended until the sclerotized plates appear as dark transverse bands (fig. 22, A and B). The thoracic and ventral regions swell most noticeably; the caudal segments remain almost unchanged. When newly emerged the planidium measures 0.20 mm. by 0.06 mm.; the fully engorged individual averages 0.45 mm. by 0.18 mm. The greatly distended body prevents any activity whatsoever, and the larva is easily dislodged from its host.

The duration of the first instar depends upon the time of pupation of the chrysopid, since feeding commences generally within several hours after the final ecdysis. The feeding period varies from 1½ to 3 days, with an average of 2 days. The mandibles (fig. 22, D) are distinct from those of later instars and measure 0.018 mm. in length.

Second Instar.—All trace of the sclerotized armor has disappeared along with the power of locomotion. The 12 body segments are faintly discernible immediately after the molt (fig. 22, C), but as the body becomes turgid with food, segmentation is obliterated. The derm is covered dorsally with numerous widely spaced microscopic granules, a double row of them extending transversly across segments 1 to 6 on the venter. As feeding proceeds, the anterior region sinks within a pitlike depression of the host derm, most of the head and segment 1 being hidden from view. The planidial sclerites which are shed frequently cling to the dorsum.

The tracheal system presents certain interesting features. Two pairs of unusually large spiracles are situated on the anterior margins of segments 2 and 4, being connected with the lateral trunks by exceptionally long tracheal branches; the anterior pair are almost dorsal in position. Blind tracheal spurs appear in segments 3, 5, 6, 7, 8, 9, and 10, and lateral branches extend both dorsally and ventrally only in segments 3, 4, 5, 6, and 7. Segment 2 and segments 8 to 12 inclusive are without ventral branches, whereas that of segment 7 extends posteriorly to accommodate most of the ventral caudal region. The extremely long spiracular connections, particularly in segment 2, would seem to be an adaptation to insure freedom for the spiracles when the larva is partially imbedded in its depression in the host derm. Bergold and Ripper (1937) show a similar tracheal arrangement in the second-instar *P. tristis* larva.

Larval increment averages 0.45 mm. by 0.23 mm. when newly molted to 1.00 mm. by 0.48 mm. at the end of the instar. The duration of the second-stage larvae is 1½ to 3 days, with an average of 2 days. The mandibles (fig. 22, E) have changed in shape, and now measure 0.026 mm. in length.

Third Instar.—In *P. tristis* and *P. hyalinus*, the third instar is characterized by seven pairs of spiracles. In *P. chrysopae* the transition from two to nine pairs of spiracles is apparently accomplished without an intervening instar.
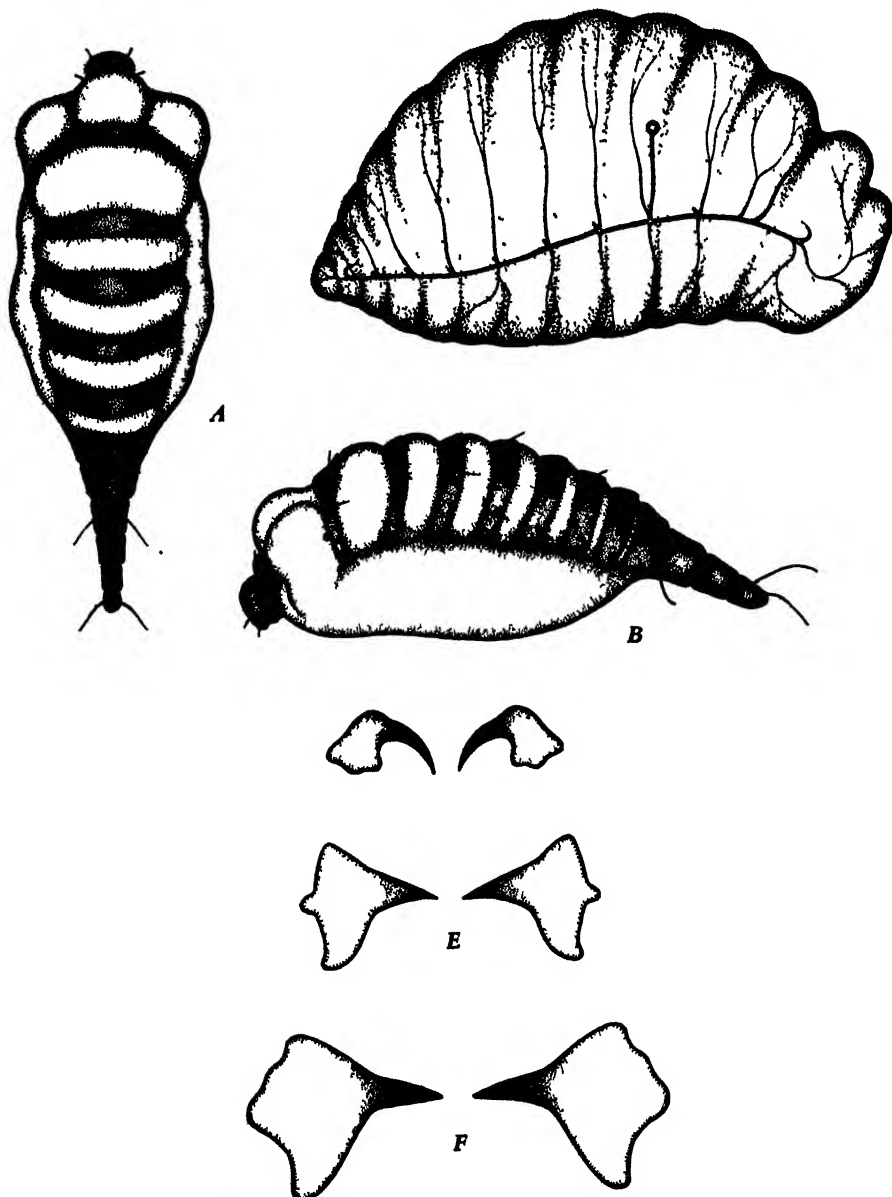
Fıg. 22. *Perılampus chrysopae* Cwfd. A. Engorged planidium, dorsal aspect. B. Engorged planidium, lateral aspect. C. Second-ınstar larva. D. First-instar mandibles. E. Second-instar mandibles. F. Third ınstar mandibles.

There are now 13 body segments; the head is entirely membranous and most peculiar in appearance, consisting anteriorly of a series of raised areas of various sizes (fig. 23, A). The bluntly rounded antennae project outward on either sidę of the median groove, and the mouth is situated between the three large rounded areas just below. No oral sensoria or setae were observed upon close examination of living material.

The thoracic segments each bear laterally a pair of teatlike protuberances, the mesothoracic pair being largest. There are nine pairs of spiracles; the first pair is situated somewhat higher as in the previous instar. There are no pronounced dorsal swellings as shown in other *Perilampus* larvae, except for the mesothoracic segment which becomes extremely distended and bulbous toward the end of the instar (fig. 23, B). Most of the internal structures are
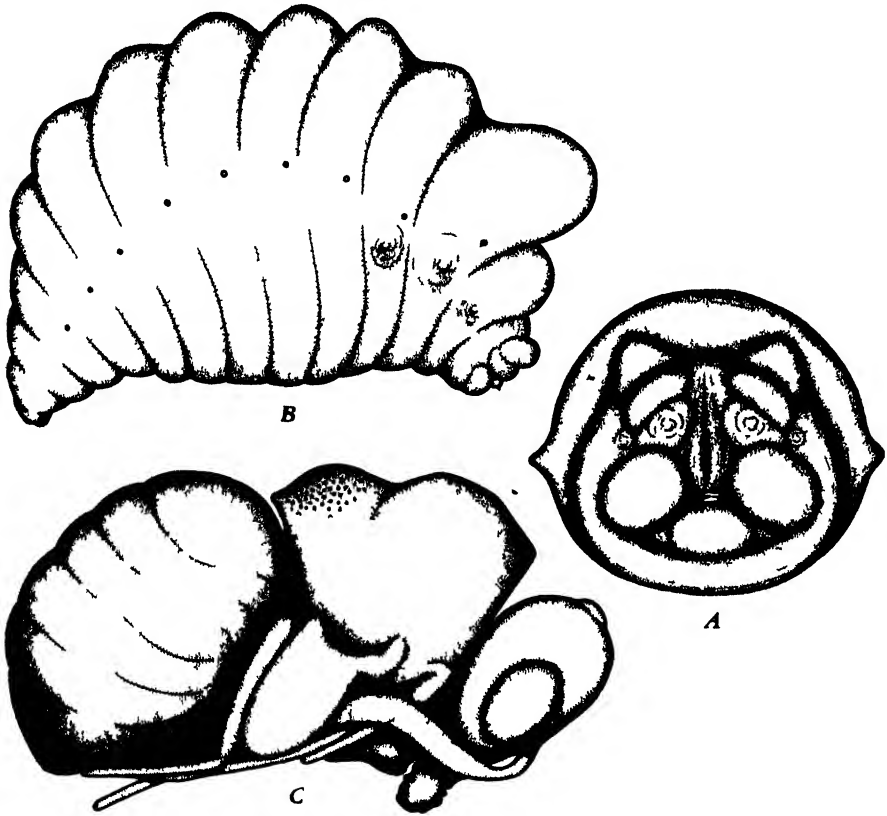
Fig. 23. *Perilampus chrysopae* Cwfd. A. Facial structure of third instar larva. B Mature third instar larva. C Pupa.

obscured by the extensive fat bodies except for a dorsal median line through which the white urate masses may be seen. The derm is minutely granular, and the body segments, particularly at the posterior end, are largely telescopic. The feeding larva frequently raises its head and even moves about over the host.

Prior to the last larval instar the *Chrysopa* pupa retains very much its original appearance. During the final instar, however, the host rapidly deteriorates into a shapeless mass. Only that which can be withdrawn through the minute feeding puncture is used as nourishment.

Mature third-instar larvae average 2.60 mm. by 1.35 mm. in size. An average of 5 days is necessary for the completion of the instar. The mandibles (fig. 22, F) are strongly chitinized and measure 0.064 mm. in length.

Pupa.—Pupation occurs 8 to 15 days after the planidium commences to feed, an average of 8 days being passed in the pupal stage.

Cocoons from which *Perilampus* have emerged are characterized by the large, jagged exit holes; the meconium is also distinctive, consisting of an irregular cream-colored mass of shining globules of various sizes which retain their spherical outlines.

Average dimensions are 2.40 mm. by 1.23 mm. The pupa of *P. chrysopae* (fig. 23, C) is identified by its compact proportions; the typical thoracic sculpturing of the adult develops long before emergence.

Overwintering occurs in the pupal stage.

Parthenogenesis and Sex Ratio.—As with the majority of chalcidoids, parthenogenetic reproduction is arrhenotokous.

The sexes were recorded from 126 *P. chrysopae* adults; 83 were females and 43 males, for a sex ratio of 1.9 females : 1 male. Martelli records 2.1 females to 1 male in *P. italicus.*

Life Cycle.—Since oviposition is indirect, a variable period must elapse before the planidium encounters its host, and, after doing so, there is a further waiting period until the *Chrysopa* pupates. Beginning in the first instar with the assumption of feeding, the life cycle is outlined as follows:

Life cycle	Extremes	Averages
	days	*days*
Egg	4 0–12 0..	6 0
First instar	1.5– 3 0....................................	2 0
Second instar	1.5– 3 0	2 0
Third instar	4 0– 7 0........	5 0
Prepupa	1 0– 2 0....................	1 5
Pupa	6 0–11 0..	8 0
Total	18 0–38.0.......................................	24 5

Since the eggs are directly exposed to changing climatic conditions, the incubation period shows the widest variation. The larval feeding period occupies approximately one-fourth of the total life cycle.

EULOPHIDAE

Tetrastichus chrysopae Cwfd.

Three species of *Tetrastichus* have been recorded from *Chrysopa* cocoons; *T. chrysopae* in California, Ohio, Virginia, and South Carolina from *C. californica* and *C. rufilabris;* and *T. pubescens* Nees is listed from *Chrysopa* sp. in Russia, and *T. blepyri* Ashm. is on record as hyperparasitic upon *Pachyneuron californicum* Gir. within the cocoon of *C. californica* in California. *T. chrysopae* is no doubt generally distributed throughout most of the United States.

The genus *Tetrastichus* is an extremely large one and exhibits great diversity as regards host relationships. Eggs, larvae, or pupae may be attacked, the immature stages being endophagous or ectophagous, and both primary and secondary parasitism is encountered. The endophagous species deposit their

eggs free within the host; they are generally somewhat arcuate and rounded at each end. The primary larvae are usually elongate with a band of minute setae encircling all or many of the segments; the head is generally prominent. Fleshy projections or setae may occur on the anal segment. In the ectophagous forms the eggs and larvae are of the generalized type without distinctive characteristics.
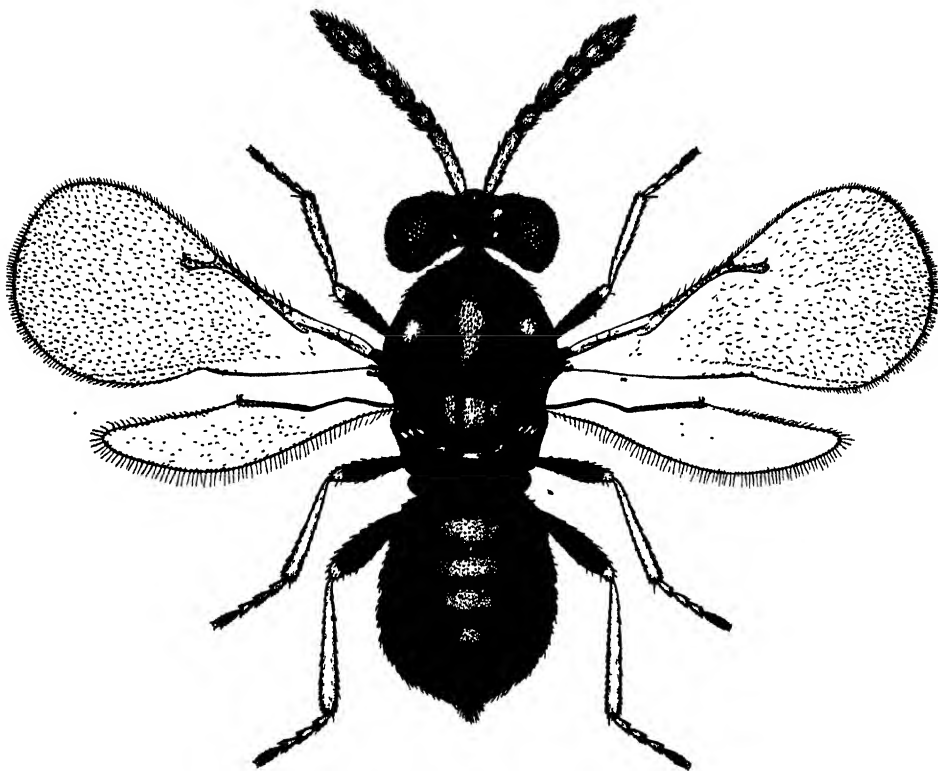
Fig. 24. *Tetrastichus chrysopae* Cwfd. Adult female.

A number of species have been investigated in some detail, many of them of considerable economic importance. Some of the more complete accounts are by the following authors: Berry (1938), Chamberlin (1925), Howard (1908), Johnston (1915), Pemberton and Willard (1918), Seitner (1927), Taylor (1937), and Urbahns (1917).

The Adult.—*T. chrysopae* was originally described as *Geniocerus chrysopae* (Crawford, 1915) from South Carolina. The female (fig. 24) is dark metallic green with the antennae brownish testaceous; femora dark brown, tibiae and tarsi, except apical joint, yellowish white. Its small size and extreme lethargy will immediately distinguish it from the other larval parasites of *Chrysopa*. The adults will live 30 to 70 days under favorable conditions.

Host Specificity.—The light or Type 1 *C. californica* larva (fig. 1, A) is the normal host of *T. chrysopae*. When oviposition occurs in the darker Type 2 larva (fig. 1, B), the eggs are killed before development progresses beyond the

blastoderm-formation stage. Phagocytic encystment becomes apparent within several days, at first as a transparent, gelatinous envelope which darkens as the encysted eggs turn black. *Chrysopa* pupae and adults were dissected which contained the typical blackish masses; they are particularly noticeable just beneath the skin against the pale-green tissues. The parasite eggs may be encysted singly or in clusters.

Peculiarly enough, these larvae when parasitized showed little or no evidence of paralyzation, although the mode of attack is identical. Furthermore, the ovipositing females were never observed to feed at the wound, but would leave the parasitized host without attempting to find the puncture. The resistance to paralyzation in the one species and not the other is most unusual.

Further evidence of the same sort is furnished by the parasitization of *C. majuscula* larvae. The results are exactly as described above; phagocytic encystment of the eggs, the absence of paralysis, and the lack of feeding at the wound are all characteristic. Apparently the host fluids are unsuitable not only for larval development but also as nourishment for the ovipositing females. *T. chrysopae* is the only larval parasite which would attack other than its normal host under natural conditions.

Oviposition.—When a *C. californica* larva is encountered, the female parasite unhurriedly mounts it, and, after a brief examination, the ovipositor is exserted and thrust directly downward into the larva. Very small to full grown host larvae are attacked with equal readiness; oviposition may occur in any part of the body, dorsal or ventral, though usually on the dorsum. The female is only with difficulty persuaded to leave its host before inserting the ovipositor, but once the act has begun it becomes impossible to force her removal. On one occasion the wings were grasped with a pair of forceps, and both host and parasite thus raised in the air without causing the ovipositor to pull free.

The *Chrysopa* larva generally runs about and attempts to dislodge the parasite with its mandibles. Owing to the female's small size and extreme tenacity, however, this objective is never accomplished. Even when oviposition occurs on the venter between the legs, and the parasite is jostled and scraped as its host dashes rapidly about, the procedure is never interrupted nor the female made less deliberate in its actions. The female remains almost motionless until near the end, when the ovipositor is generally thrust up and down with a restricted probing movement. From 11 to 21 minutes elapse with the ovipositor imbedded; an average of 15.5 minutes was obtained.

After 5 to 10 minutes the chrysopid becomes noticeably less active, and several minutes later a partial or complete paralysis has set in. When completely paralyzed the host is entirely immobile and may be rolled about; only the legs exhibit a slight quivering motion. Very small to half-grown larvae are almost invariably entirely paralyzed, whereas mature individuals may sometimes be only partially paralyzed; in such instances the *Chrysopa* is able to crawl slowly when stimulated. Egg deposition is probably effected subsequent to inactivation, the paralytic secretion being injected during the first phase.

Immediately the ovipositor is withdrawn, the female moves backward until it finds the puncture. It applies the mouth parts and then feeds upon the exud-

ing fluids for 3 to 8 minutes. Feeding invariably followed oviposition when the normal host was attacked. Even those individuals which had oviposited regularly for several weeks fed after each laying. The males, unlike the females, fed only on honey solution. In *T. coccinellae* Kurd. (Oglobin, 1913), a larval parasite of coccinellids, the females feed at the wound, although paralysis was not mentioned.

Host paralysis is apparently an adaption to permit adult feeding. Generally within about 5 minutes after the parasite has left, the *Chrysopa* larva fully recovers its normal faculties. Even when very small larvae are attacked simultaneously by several females, full recovery is assured. The host remains paralyzed from 12 to 21 minutes, with an average of 16 minutes. Approximately 25 minutes elapse from the insertion of the ovipositor until the *Chrysopa* is fully recovered.

At each oviposition 2 to 18 eggs are laid, with an average of 9. They are deposited in clusters just beneath the host derm. Host size apparently does not influence the number of eggs laid. Females will oviposit in previously parasitized larvae apparently without limit; superparasitism thus results in the ultimate death of both host and parasites.

Although not definitely ascertained, the reproductive capacity is undoubtedly high. When supplied regularly with *Chrysopa* larvae, oviposition occurs at an average rate of once per day. Assuming an average of 9 eggs per oviposition over a period of 30 days, a theoretical capacity of 270 is obtained.

In *T. asparagi* (Johnston, 1915), oviposition occurs in the host egg, the full grown larvae emerging from the mature host larva.

Egg.—The deposited egg (fig. 25, A) averages 0.21 mm. by 0.06 mm. through the large end. It is whitish in color with a smooth, glistening chorion; there is no appreciable increase in size during incubation. Eclosion generally occurs 3 to 5 days from oviposition ($3\frac{1}{2}$ days at 75° F.), the larva emerging at the broad or cephalic end.

Larvae.—Three larval instars occur as in the other species of *Tetrastichus* which are recorded in detail.

First Instar.—The newly emerged larva (fig. 25, B) is an exceedingly small, delicate individual with a prominent head and 13 body segments, the first of which is the smallest and incomplete ventrally. A row of minute colorless setae encircle all but segments 1 and 13, and are barely discernible under high magnification. The respiratory system is only slightly developed; the threadlike tracheal trunks bear nine pairs of microscopic, lateral branches. Larval mandibles, although present, could not be accurately measured owing to their extreme transparency and minute proportions.

At first short and broad in outline, the larva soon becomes more elongate, increasing to 0.55 mm. by 0.18 mm. just preceding ecdysis. At 75° F., the first instar was $1\frac{1}{2}$ days in duration, the initial molt occurring 5 days from oviposition.

Second Instar.—The larva is now long and slender and without setae (fig. 26, A), and the tracheal system has developed extensive lateral branches in addition to short spiracular spurs in segments 2, 3, 5, 6, 7, 8, 9, and 10. Those

of segment 4 are either vestigial or entirely lacking. Owing to the very small larval mandibles throughout, the instars may best be distinguished on the basis of tracheal development.

The duration of the second instar depends upon the rate of host development. If the *Chrysopa* larva has spun its cocoon, the stage is completed in approximately 24 hours at 75° F. Should the host be parasitized when very small, however, parasite development is retarded in the second instar until it
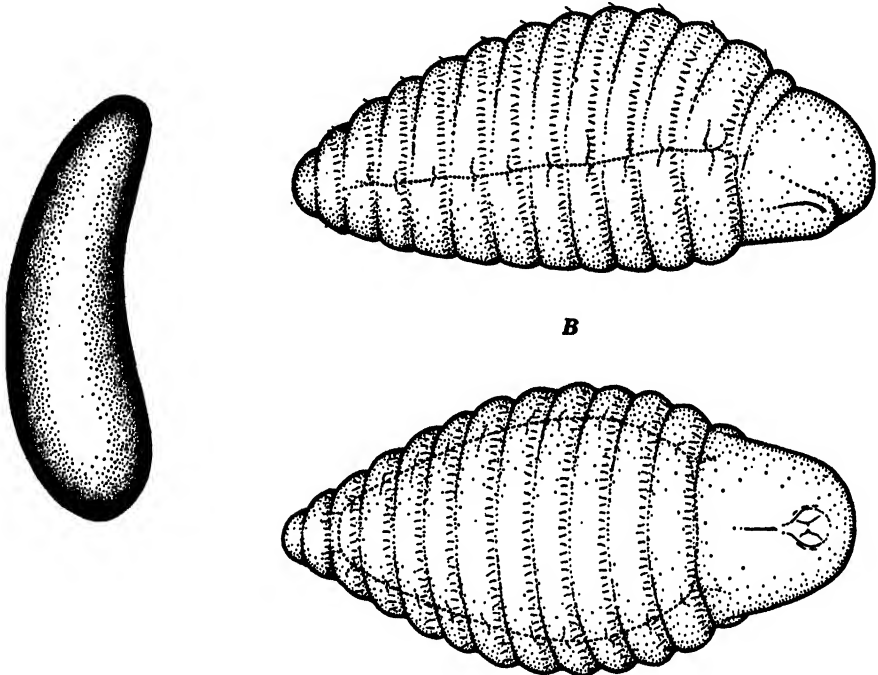
Fig. 25. *Tetrastichus chrysopae* Cwfd. A. Deposited egg. B. Newly emerged first-instar larva, lateral and ventral aspects.

has spun. Metamorphosis is not inhibited indefinitely, however. A maximum of 12 days elapsed from oviposition during which the host larva failed to construct its cocoon; on the following day, the *Chrysopa* was found dead, and upon dissection yielded a number of newly molted third-instar larvae. The second instar had been prolonged from a normal of 1 day to a maximum of approximately 7 days. In such instances larval growth proceeds at a uniformly slow rate throughout the instar. This phenomenon is apparently regulated by obscure physiological changes within the host prior to spinning. Pupation is not concerned, for occasional parasitized individuals will pupate before death occurs.

At the end of the instar the larvae have increased to an average of 0.90 mm. by 0.26 mm. The delicate mandibles measure 0.017 mm. in length.

Third Instar.—In the final instar the larva (fig. 26, B) closely resembles that of the previous stage. Only eight pairs of functional spiracles appear, however, in those segments which bore spiracular spurs in the second instar. The third

tracheal branch (in segment 4), though generally as long as the others, invariably ends blindly. *T. brevistigma* (Berry, 1938) also possesses but eight pairs of spiracles in the final instar; the arrangement is identical to that of *T. chrysopae*.

The third-instar larva is also characterized by the presence of a delicate, tightly fitting membrane which envelops all but the head and a portion of segment 1; it apparently represents the persistent second-instar exuvia. What
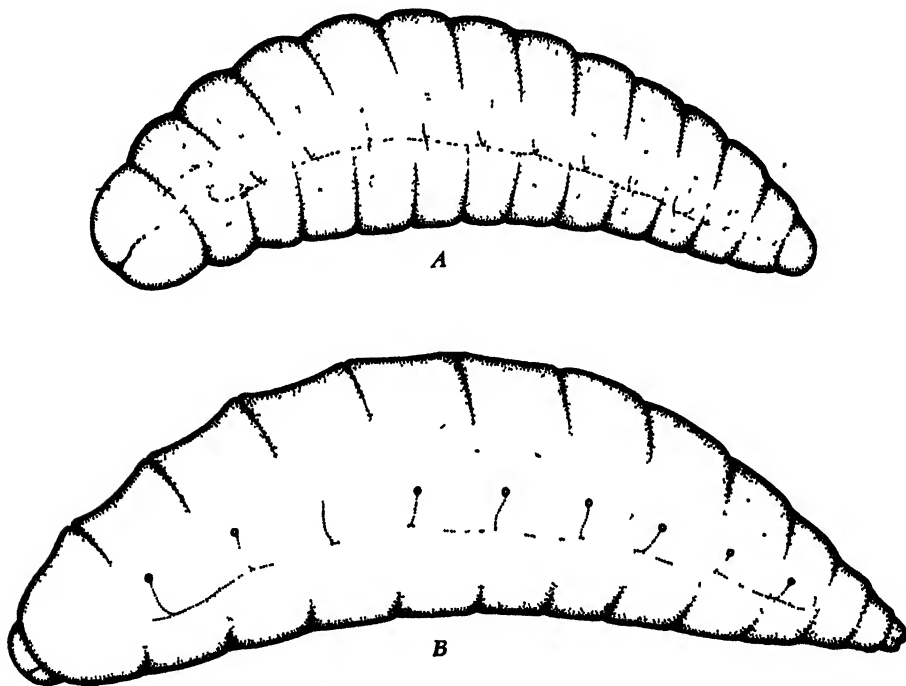
Fig 26 *Tetrastichus chrysopae* Cwfd. A. Second instar larva. B Third instar larva.

appears to be a similar arrangement is noted by Urbahns (1917) in *T. bruchophagi*. As in *C. compressicornis*, its apparent function is to protect the open spiracles when the parasite is surrounded by host fluids.

The host is killed at the beginning of the instar. Within 24 hours the larvae may be seen moving about inside, and at the end of a similar period the host contents have been entirely consumed and the *Chrysopa* derm is distended with numerous swellings, each of which represents a *Tetrastichus* larva. The larvae emerge 1 to 2 days later, leaving the enveloping membranes within. Following a quiescent interval of similar duration, the prepupal period commences; it averages 2 days. Thus the third instar (excluding the prepupa) is about 4 days, less than two of which are occupied in feeding.

Mature larvae average 2.10 mm. by 0.64 mm. The mandibles are somewhat more distinct, and measure 0.025 mm.

Pupa.—A small part of the meconium is retained after pupation, and may be dissected from the abdomen in the form of a thick, yellowish mass. Newly

emerged adults still contain this material, but after ovipositing it largely disappears. Pemberton and Willard (1918) found that in *T. giffardianus* the greater part of the meconium was passed by the adult immediately upon emergence.

Following a pupal period of 6 to 11 days, the adults all emerge, within 24 hours, from 1 to 3 exit holes cut in various parts of the *Chrysopa* cocoon.

Number per Host and Sex Ratio.—A total of 309 *C. californica* cocoons were parasitized by *T. chrysopae*, of which 208 were from cotton, 100 from walnut, and 1 from citrus. An average of 12.3 adults was obtained per host cocoon; from 1 to 33 parasites emerged from individual cocoons. Seitner (1927) bred as many as 2,000 *T. xanthopus* per pupa of the Pine moth.

From 50 cocoons selected at random there emerged 443 females and 215 males, for an approximate ratio of 2 females to 1 male. Four of them produced solely male parasites, whereas nearly all of those maturing (less than 7 *Tetrastichus*) resulted in all females (7 cocoons). In the average group (represented by 19 cocoons which gave rise from 10 to 15 *Tetrastichus*), the proportion of females increased so that the ratio was 3.1 : 1.

Among most other species of *Tetrastichus* the sex ratio ranges from 3 : 1 to 5 : 1 with females predominating. However, no males were observed by Johnston (1915) in *T. asparagi*, and males appeared but rarely in *T. brevistigma* (Berry, 1938).

Life Cycle.—When the host larva spins its cocoon prior to the second parasite instar, the life cycle is as follows:

Life cycle	Extremes	Averages
	days	*days*
Egg	3.0– 5.0.	3.5
First instar	1.0– 2.0.	1.5
Second instar	1.0– 1.5.....	1.0
Third instar	3.5– 6.0.. .	4.5
Prepupa	1.5– 3.0...	2.0
Pupa	6.0–11.0...	7.5
Total	16.0–28.5........	20.0

Only two of the many chrysopids parasitized in the laboratory succeeded in pupating before death occurred, parasitization being accomplished in the mature larvae just before spinning.

PTEROMALIDAE

Pachyneuron californicum Gir.

P. californicum is the only member of the genus listed from *Chrysopa*. In addition to Cole's (1933) California reference, the species is herein recorded as a hyperparasite of both *C. californica* and *C. majuscula*. Smith (1917) mentions *Pachyneuron* sp. from the cocoons of the hemerobiid, *Sympherobius californicum*.

The species of *Pachyneuron* are predominantly hyperparasitic in habit, although several are known to develop as primary parasites. The Diptera and Homoptera are most often subject to attack; *Pachyneuron* is especially noted as a hyperparasite of aphids. All the investigated species are ectoparasitic, and exhibit great similarity in the immature stages. The eggs are covered with minute tubercles except on the smooth ventral surface, the first-instar larvae generally bear four pairs of spiracles, and the last instar is of the generalized
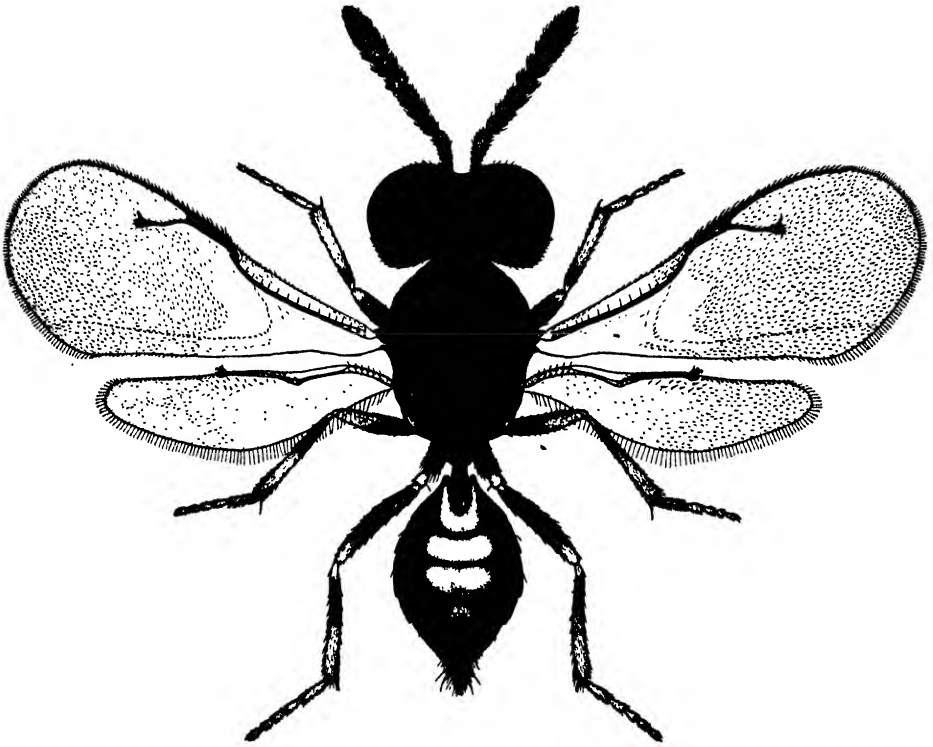
Fig. 27. *Pachyneuron californicum* Gir. Adult female.

type with nine pairs of spiracles. Most species are gregarious, and the ovipositing females commonly feed upon the exuding host fluids. Howard and Fiske (1911) have reared *P. gifuensis* Ashm. from gipsy moth eggs upon the egg parasites *Anastatus* and *Schedius*.

Among those who have contributed to the biology of the genus are the following: Faure (1923), Haviland (1922), Kamal (1926), Silvestri (1919), and Spencer (1926).

The Adult.—*P. californicum* was originally described from California by Girault (1917); the black, large-headed female (fig. 27) is readily distinguishable. The males have white legs, except on the coxae and the proximal half of the posterior femur, and the scape is nearly whitish.

During the entire study only 13 field-collected cocoons produced *P. californicum;* 8 of them emerged from *C. californica* and 5 from *C. majuscula.*

Because of the absence of distinctive biological features, the present account is brief.

Oviposition.—After thoroughly investigating the interior of the *Chrysopa* cocoon with the ovipositor, deposition occurs externally upon the primary inhabitant. Eggs were also laid in mummified *Chrysopa* larvae inhabited by *Isodromus* pupae.

Oviposition is never effected upon parasite larvae still surrounded by host fluids. In the laboratory the following species served as hosts: *Isodromus niger*,
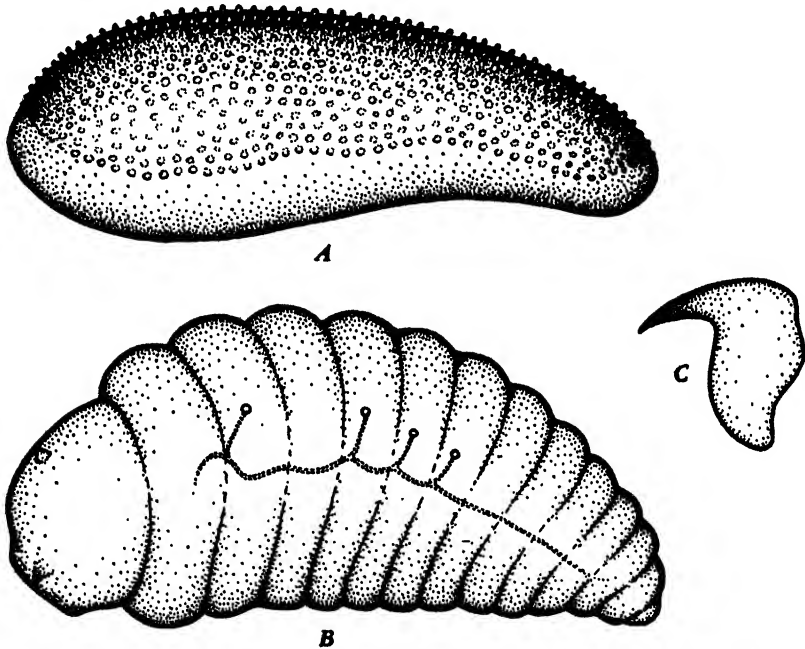
Fig. 28. *Pachyneuron californicum* Gir. A. Deposited egg. B. First-instar larva.
C. First-instar mandible.

I. iceryae, Chrysopophagus compressicornis, Hemiteles tenellus, Dibrachys cavus, and development was even completed upon individuals of its own species.

Ovipositing females fed extensively through delicate feeding tubes constructed in the usual manner. Feeding may also occur without the deposition of eggs. Faure (1923) found that the same feeding tube was utilized by different females in *Pachyneuron* sp. which parasitizes syrphids.

Egg.—The egg (fig. 28, A) is entirely similar to that of the other species investigated. The smooth ventral surface adheres lightly to the host derm. Average dimensions were 0.28 mm. by 0.11 mm. Eclosion occurs in 2 to 4 days.

Larvae: first instar.—The prominent head capsule and 13-segmented body, together with the usual four pairs of spiracles, are typical of the first-instar larva (fig. 28, B). An average of 2 days is spent in the instar. The mandibles measure 0.015 mm. in length (fig. 28, C).

Final Instar.—In the final instar (fig. 29, A) the larva has attained the complete nine pairs of spiracles, and each of the thoracic segments possesses

laterally a small, rounded raised area; the derm immediately adjacent on segment 1 is finely roughened. Growth is rapid, and the larva is capable of extreme distention and contraction. A maximum size of 1.60 mm. by 0.73 mm. is achieved, following a feeding period of approximately 2 days. The mandibles (fig. 29, B) average 0.045 mm.

Pupa.—The pupa (fig. 29, C) is distinguished by its large head and roughened derm; when mature the granulations are most evident, being particularly
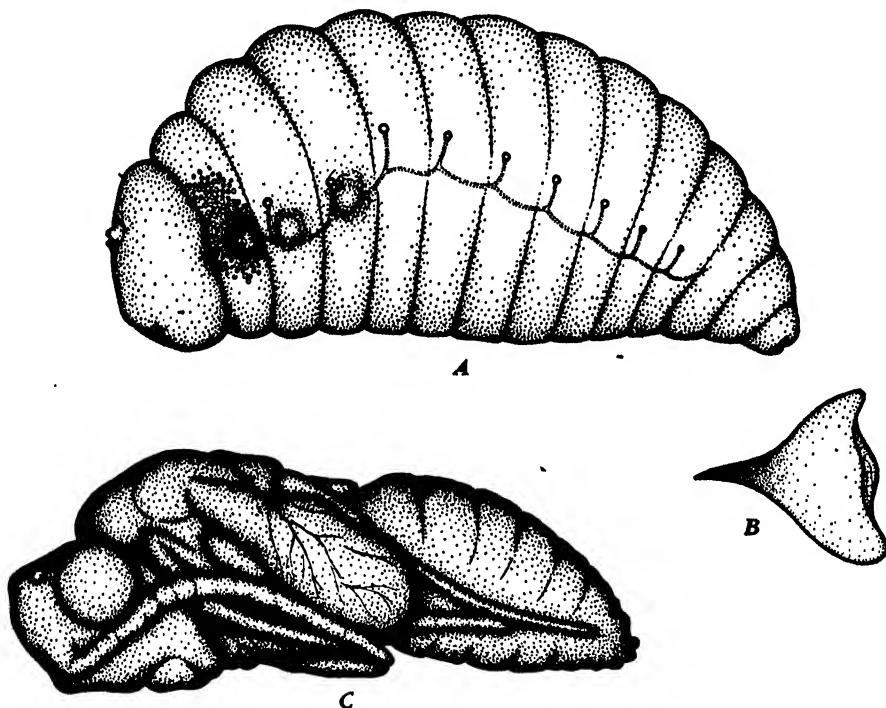
Fig. 29. *Pachyneuron californicum* Gir. A. Mature third-instar larva.
B. Third-instar mandible. C. Pupa.

noticeable in bands encircling the anterior half of each abdominal segment. Pupation occurs beside the shriveled host remains within the *Chrysopa* cocoon.

Number per Host and Life Cycle.—A total of 22 adults emerged from the 13 host cocoons for an average of 1.7 *Pachyneuron* per cocoon; 1 to 5 parasites issued from individual cocoons.

The following information was secured at laboratory temperatures:

Life cycle	Extremes	Averages
	days	*days*
Egg	2.0– 4.0	2.5
Larva	7.0–11.0	8.5
Prepupa	1.5– 2.5	2.0
Pupa	6.5–12.0	8.0
Total	17.0–29.5	21.0
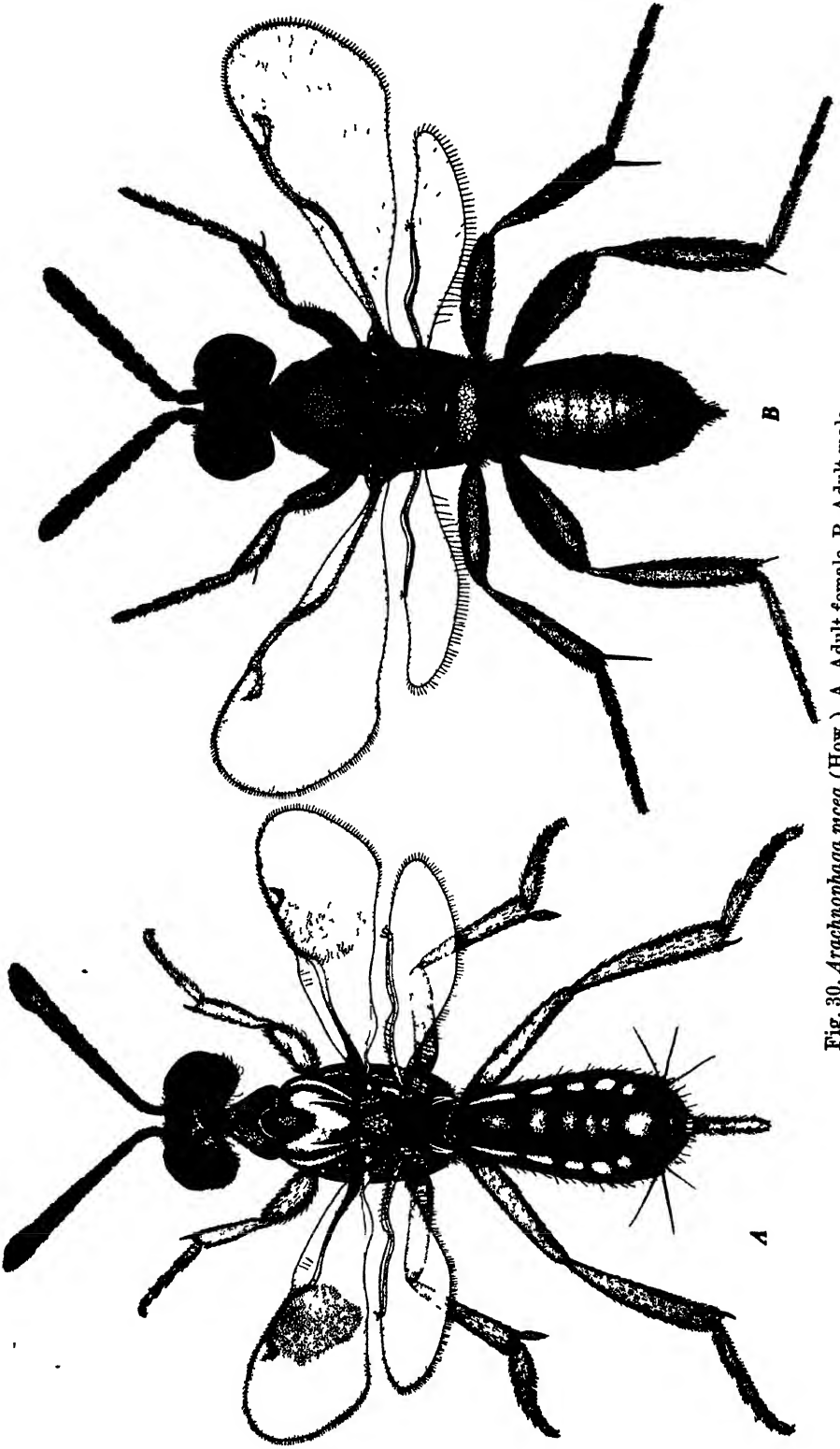
Fig. 30. *Arachnophaga picea* (How.). A. Adult female. B Adult male.

<center>*Dibrachys cavus* Wlk.</center>

This pteromalid (formerly *D. boucheanus* Ratz.) is probably the commonest and most widely distributed of all hyperparasites. Its hosts are both numerous and varied, and, as in the present investigation, it has occasionally been reared as a primary parasite.

D. cavus is predominantly a hyperparasite of *C. californica;* only 8 of the 142 field-collected cocoons from which it issued were *C. majuscula.* Records were obtained from walnut, apple, and orange; on walnut it ranked sixth in abundance, accounting for 3.7 per cent of the total parasitism. In the laboratory the majority of cocoons subjected to parasitization failed to produce *D. cavus,* because of the excessive feeding habits of the adult females. That such is often the case in nature was indicated by the presence of numerous blanks containing deflated host larvae and pupae.

Since the biology of *D. cavus* was apparently similar to that of most pteromalids, and since considerable information already exists in the literature, no further study was made.

<center>EUPELMIDAE</center>

<center>*Arachnophaga picea* (How.)</center>

A. picea is normally a spider parasite. Davidson (1894) has reared it from the egg cocoons of *Agriope argentata* on *Opuntia* cactus in southern California and on Catalina Island off the coast, the larvae developing as egg predators. The same species was the subject of an ecological study by Weese (1930) in Oklahoma, who reared it from the eggs of the spider *Epeira gibberosa.* Although originally described as *Eupelmus piceus* Riley (Howard, 1890), Ashmead subsequently (1901) made it the type for the new genus *Arachnophaga.*

The present record is the first outside the Arachnida; *A. picea* is herein recorded as a hyperparasite of *C. californica.* The species is probably capable of development upon various hosts which either spin or occur within silken cocoons. *Arachnophaga* sp. from *C. lateralis* in Florida is probably the same species. *Eupelmus chrysopinus* Perk. has been listed from the cocoons of *Anomalochrysa* spp. in the Hawaiian Islands.

The Adult.—The female (fig. 30, A) is reddish brown and black with metallic reflections; the wings are hyaline except for a fuliginous area below the marginal vein; ovipositor prominent. The male (fig. 30, B) is entirely dissimilar and considerably smaller.

Although the females are slow and deliberate, the males are nervously active and move with short, jerky motions. The wings are flitted in the manner of certain mud dauber wasps. The females are extremely hardy, having lived in the laboratory for as long as 121 days; the males are much shorter lived.

Oviposition.—Eggs may be deposited upon any of the primary or secondary parasites of *Chrysopa,* and even upon individuals of its own species. The degree of parasitism is limited only by the available food supply necessary to mature individual larvae. The eggs adhere to the inner surface of the host cocoon; with *Isodromus* spp., deposition occurs within the parchmentlike sheaths. There is

no webbing over the eggs as in many eupelmids. A preoviposition period of 5 to 15 days ensues, with oviposition extending over a long period. Only a few mature ovarian eggs are ever present at one time.

A virgin female commenced oviposition 9 days after emergence. Within 76 days 27 eggs were deposited for an average of 0.35 eggs per day; a maximum of 5 eggs per day was laid following an 8-day interval without hosts. The female
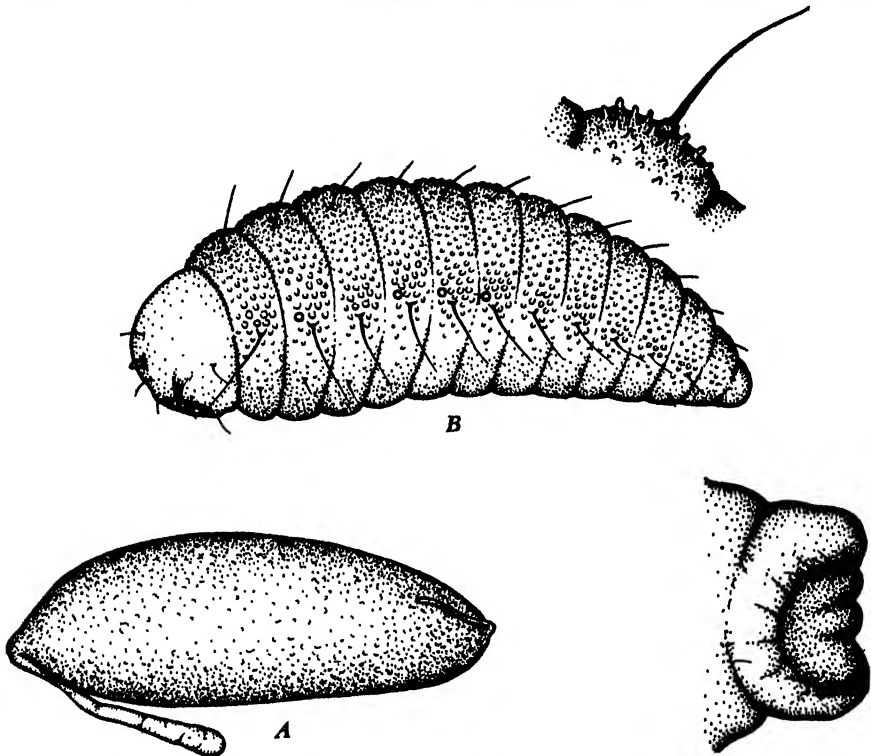
Fig. 31. *Arachnophaga picea* (How.). A. Deposited egg. B. First-instar larva showing enlarged latral seta and dermal tubercles. C. Anal "sucker" of first-instar larva.

lived for 91 days. Eggs are also occasionally deposited upon *C. californica* pupae, but larval development never progresses beyond the first instar.

A. picea feeds extensively at the ovipositor punctures, sometimes without leaving eggs. Upon opening the *Chrysopa* cocoon, the white threadlike feeding tubes may be seen within.

Egg.—The deposited egg (fig. 31, A) is translucent white with a minutely roughened chorion, and is characteristic of the majority of eupelmids; the petiole varies considerably in shape. Average dimensions are 0.57 mm. by 0.18 mm. Eclosion occurs in 3 to 6 days.

Larvae.—The usual five instars were identified; only the first and fifth stages will be described.

First Instar.—The newly emerged larva (fig. 31, B) measures 0.60 mm. by 0.16 mm., the head capsule (fig. 33, A) averaging 0.13 mm. in width. The derm is coarsely roughened, particularly in the midlateral regions, where the peg-

shaped dermal projections are most prominent. Paired dorsal and lateral setae occur on most segments in addition to three pairs of minute ventral setae on the thoracic segments; lateral setae are longest, the first pair extending forward. The anal segment is modified ventrally as a sucker (fig. 31, C) similar to that of the *Perilampus* planidium. Progress is also effected by means of a looping movement, the larva frequently changing position on its host. The tracheal system is peripneustic with four pairs of spiracles on segments 2, 4, 5, and 6; spiracular spurs are present on segments 3, 7, 8, 9, and 10.
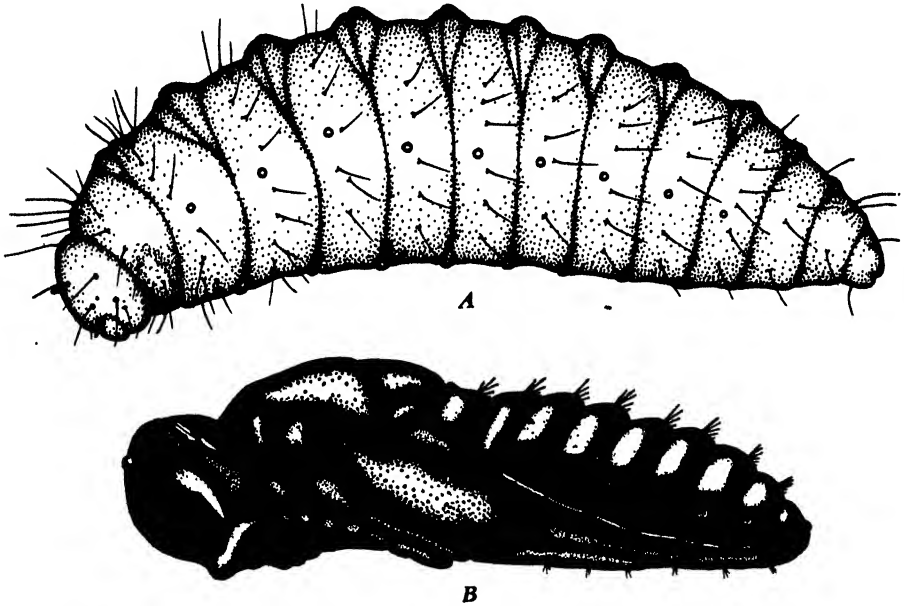
Fig. 32. *Arachnophaga picea* (How.). A. Mature fifth-instar larva. B. Male pupa.

Following a feeding period of 1 to 3 days, an average size of 0.90 mm. by 0.28 mm. is attained. The mandibles (fig. 33, C) are entirely different from those of subsequent instars, and measure 0.023 mm. in length.

Fifth Instar.—The last-instar larva (fig. 32, A) cannot be confused with that of any other *Chrysopa* parasite. Numerous yellowish setae adorn the body, and most segments are marked dorsally and, to a lesser extent, ventrally by characteristic swellings. The larva rarely moves from its original feeding site, although the head is frequently raised and moved about. Nine pairs of spiracles are present on segments 2 to 10 inclusive. The mouth parts and facial region (fig. 33, B) differ widely from the first instar; the serrate oral plate is characteristic of most eupelmids.

An average of 5 days is spent in the instar, 3 of which are occupied in feeding. Mature larvae averaged 3.0 mm. by 0.85 mm. Those larvae which will produce females are noticeably larger. The mandibles (fig. 33, C) measure about 0.072 mm.

Pupa.—The male pupa (fig. 32, B) is coal black in color even when newly evolved, the glistening surface being sparsely covered with minute granula-

tions except on the head and abdomen. Each abdominal segment is encircled with a band of short, stiff, erect yellowish hairs. Shortly before hatching, the abdomen becomes flattened dorsally. The female pupa lacks setae and is non-melanized.

Average dimensions are 2.35 mm. by 0.81 mm. Approximately 13 days are passed in the pupal stage under average conditions.

Number per Host and Sex Ratio.—*A. picea* was one of the least abundant parasites of *C. californica*. A total of 13 adults (8 females and 5 males) emerged from field-collected cocoons, for an average of 1.3 per cocoon. A maximum of 3 parasites issued from 1 cocoon. Two other cocoons produced one each of *Isodromus iceryae* and *A. picea*.

Life Cycle.—The following data were secured from individuals reared under laboratory conditions:

Life cycle	Extremes	Averages
	days	*days*
Egg	3– 6..	4.0
First instar	1– 3..	2.0
Second instar	1– 2..	1.0
Third instar	1– 2..	1.0
Fourth instar	1– 2..	1.0
Fifth instar	4– 9..	5.0
Prepupa	1– 2..	1.5
Pupa	11–18..	13.0
Total	23–44..	28.5

TRICHOGRAMMATIDAE

Trichogramma embryophagum (Htg.)

Although no extensive collections of *Chrysopa* eggs were made, *T. embryophagum*[3] was reared on several occasions from the eggs of *C. californica* on citrus. It was never obtained from *C. majuscula* eggs collected on this and other host plants. From 1 to 3 parasites issued per host. Since considerable information already exists on the biology of *Trichogramma*, no attempt was made to study the species.

Trichogramma minutum Riley has been reared from the eggs of *C. oculata* and *C. albicornis* in Canada, and from *Anomalochrysa* spp. in the Hawaiian Islands. Moffat (1901) mentions the rearing of a minute "Ichneumon" from *Chrysopa* eggs in England; from his description the parasite was undoubtedly *Trichogramma*.

The egg parasite *Telenomus chrysopae* Ashm. may also occur in California, although it was not obtained from the relatively few eggs collected.

ICHNEUMONIDAE

Chrysopoctonus patruelis Cushm.

The genus *Chrysopoctonus* contains five species (Cushman, 1924), all of which are parasites of *Chrysopa* in the United States and Canada. In a previous pub-

[3] Determined by Dr. S. E. Flanders.

lication (Cushman, 1919) the genus was erected with *Otacustes atriceps* Ashm. as the type, it having been described along with *O. chrysopae* Ashm. from cocoons of *Chrysopa oculata* Say on cotton in Mississippi (Ashmead, 1894). Apparently the earliest record of a species now considered as *Chrysopoctonus* is that of *Hemiteles hemerobii* Ashm. reared from "*Hemerobius* cocoon" (Ashmead, 1890), now synonymized with *C. rileyi* (Ashm.).
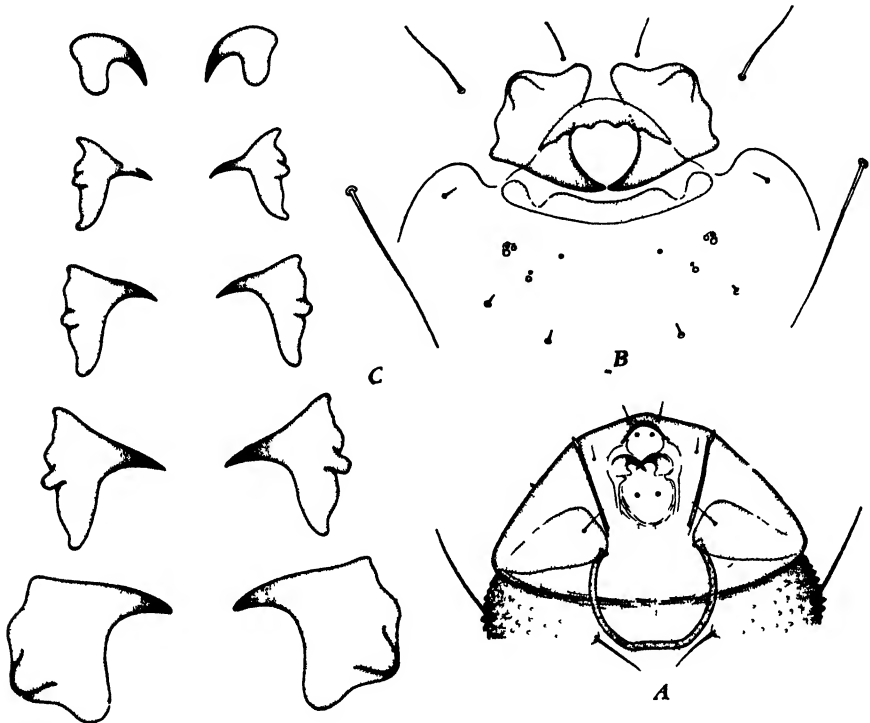
Fig. 3. *Arachnophaga picea* (How.). A. Facial structures of first-instar larva. B. Mouth parts of fifth-instar larva. C. Larval mandibles of first to fifth instars.

C. patruelis is the sole western representative of the genus, being recorded only from *Chrysopa californica* in California. I have reared it experimentally from *Eremochrysa punctinervis* McLach.

The closely related genus *Brachycyrtus* is probably similar in its host relations, since one of the five species, *B. nawaii* (Ashm.), has been reared from *Chrysopa* in the Philippine Islands (Cushman, 1936).

The present account is the first on the biology of any member of the genus.

The Adult.—The female (fig. 34) is characterized by its reddish-black coloration, prominent ovipositor, and hyaline wings. *Hemiteles tenellus* has distinctly dark-banded forewings.

This cryptine is very hardy; adults have lived as long as 55 days in the laboratory.

Oviposition.—The abdomen is raised until the ovipositor contacts the host cocoon immediately below the thorax. After bracing itself solidly, drilling is

commenced by moving the stylets rapidly up and down upon one another. With the ovipositor thoroughly inserted, a series of probing motions ensue. Pupae, prepupae, or resting larva are acceptable with no apparent preference. Oviposition even occurs upon mature pupae.
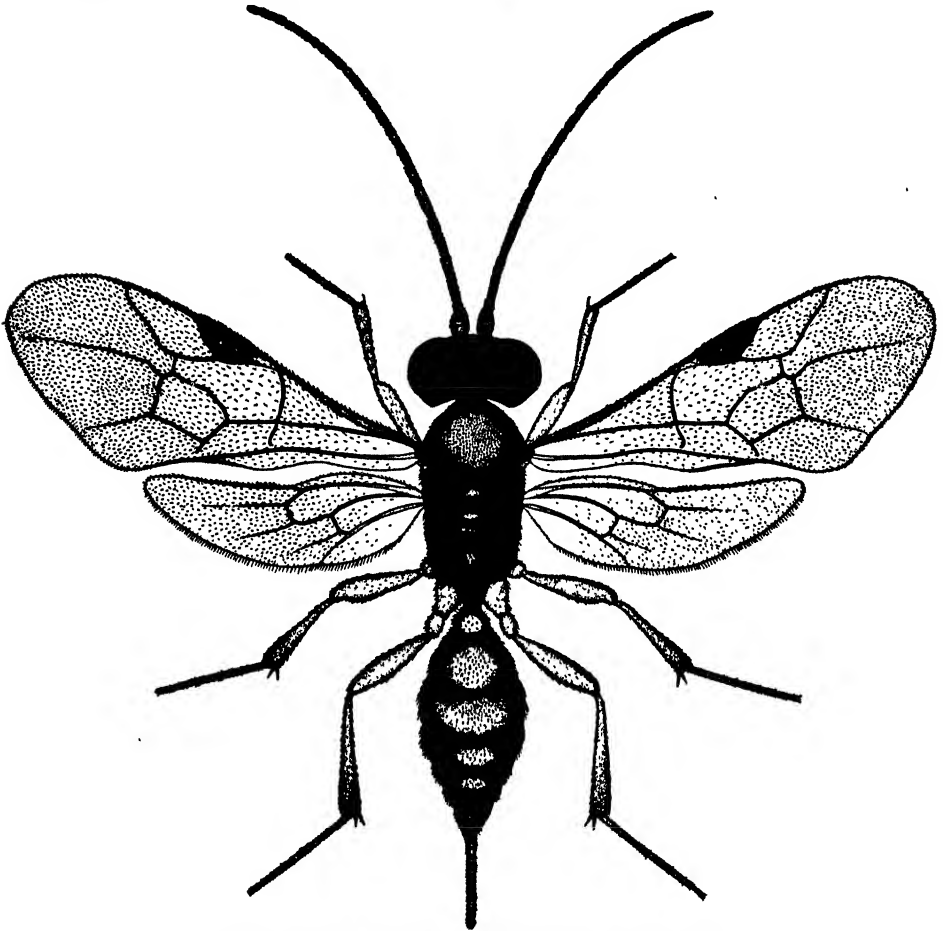
Fig. 34. *Chrysopoctonus patruelis* Cush. Adult female.

A paralysis is produced from which the host does not recover. Oviposition was never completed upon nonparalyzed individuals, although some paralyzed hosts were found without parasite eggs. The ovipositor is jabbed forcibly into the *Chrysopa;* as the paralyzing fluid is injected, movement gradually subsides and finally ceases altogether. Following a brief examination, the egg is deposited either upon the host itself or in contact with the inner surface of the cocoon. The entire procedure occupies 3 to 12 minutes.

Although development was never completed on *C. majuscula*, eggs were frequently deposited, and paralysis resulted in several instances. The majority of newly hatched larvae died apparently without feeding; none advanced beyond the first instar.

In an effort to determine whether *Chrysopoctonus* will ever develop hyper-parasitically, a series of cocoons containing various primary species was offered. *Chrysopoctonus* failed to issue from any of them. Eggs were also transferred to *Isodromus* larvae and pupae in glass cells, but although several larvae fed and increased considerably in size, metamorphosis was never completed.

Generally within 1 or 2 days after paralyzation, the host becomes flaccid and yellowish. Sometimes the dorsal vessel pulsates feebly for several days; other-wise death coincides with the flaccid stage. If the parasite egg is removed, the
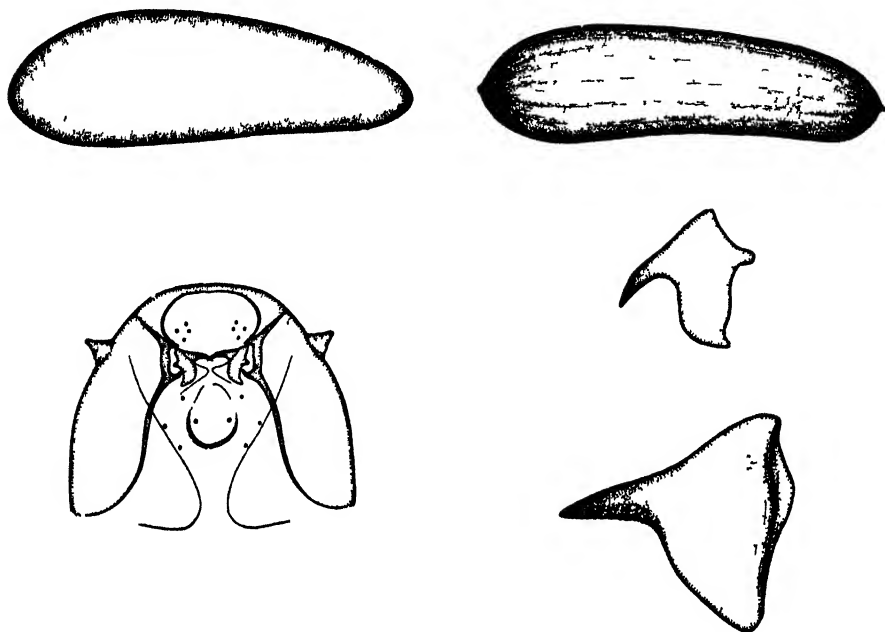
Fig. 35. *Chrysopoctonus patruelis* Cush. A. Ovarian egg. B. Deposited egg.
C. First-instar mouth parts. D. First- and fifth-instar mandibles.

chrysopid remains in a preserved condition for many days. This fluid serves permanently to inactivate the host and prevent injury to the eggs and larvae, to stop development, thus insuring nourishment for the larvae, and to preserve the food supply from contamination.

A preoviposition period of 3 to 7 days is required.

Egg: ovarian egg.—The ovarian egg (fig. 35, A) is dull white in color and measures approximately 0.702 mm. by 0.234 mm. Only a few mature eggs are found per female, although numerous immature ova occur in the tubular avarioles.

Deposited Egg.—At deposition the minutely roughened chorion exhibits faint longitudinal ridges; a small projection occurs at either end (fig. 35, B). The broad end has decreased to approximately 0.195 mm. in width.

Although more than one egg may be deposited per host, only one adult will mature. The incubation period varies from 1 to 2 days.

Larvae.—Five instars were distinguished; only the first and fifth will be considered.

First Instar.—The primary larva is quite similar to that of *Hemiteles tenellus* (see fig. 37, A) with the following exceptions: the head is narrower and more elongate in proportion (fig. 35, C), the larval antennae are short and broad basally, being conical in outline, and the dermal armature is less pronounced than in *Hemiteles*. Minor differences also exist in the mouth parts. The tracheal system is identical in both species, and will be described for *H. tenellus*.

Eclosion is effected at the broad end of the egg. After wandering about for several hours, feeding is begun ectoparasitically at any point on the host body. The entire feeding period is generally passed at or near the original site of attachment.

Growth is rapid, the primary larva increasing from 0.67 mm. by 0.20 mm. to 0.95 mm. by 0.31 mm. in 1 to 1½ days. The chitinized head capsule, which in the newly emerged larva is as broad as the body, averages 0.180 mm. in width. As feeding proceeds, the dermal tubercles become less apparent; under the microscope they appear as tiny, transparent raised dots.

The mandibles (fig. 35, D) are distinct from those of subsequent instars and measure 0.036 mm. in length.

Fifth Instar.—The last instar is also quite similar to that of *Hemiteles tenellus* (see fig. 38, A); the antennal papillae, however, are still short and conical, and the dermal armature is less distinct than in *Hemiteles*. On the vertex there are a pair of raised, elongate papillate areas which are melanized and quite obvious even at low magnifications (fig. 36, A). The oral structures present additional diagnostic features.

An average increment of 2.70 mm. to 3.40 mm. takes place in 3½ to 6 days; the head capsule now averages 0.56 mm. in width. The mandibles (fig. 35, D) are large and heavily chitinized with the points minutely ridged on one side. They measure 0.069 mm. in length.

After feeding for approximately 2 days, the larva lies quiescent for a similar period before commencing to spin. Although the cocoon generally consists only of a delicate silken partition separating the parasite from the host remains below, it may occasionally be dissected from the walls of the *Chrysopa* cocoon as an entire envelope.

In both *C. patruelis* and *Hemiteles tenellus*, overwintering occurs as mature larvae. The meconium is voided in the form of numerous rounded, elongate, grayish pellets.

Pupa.—Pupation occurs 8 to 16 days from oviposition, following a larval feeding period of 4½ to 9 days. The pupa (fig. 36, B) averages 3.10 mm. by 1.70 mm. Emergence is effected through a round, jagged exit hole at either end of the cocoon. The duration of the pupal stage is 5 to 9 days.

Sex Ratio and Parthenogenesis.—From field collections 162 *C. californica* cocoons were parasitized by *C. patruelis;* 93 were females and 69 males, for a sex ratio of 1.3 : 1.

The progeny of unmated females are males, whereas in *Hemiteles tenellus* the male is unknown.
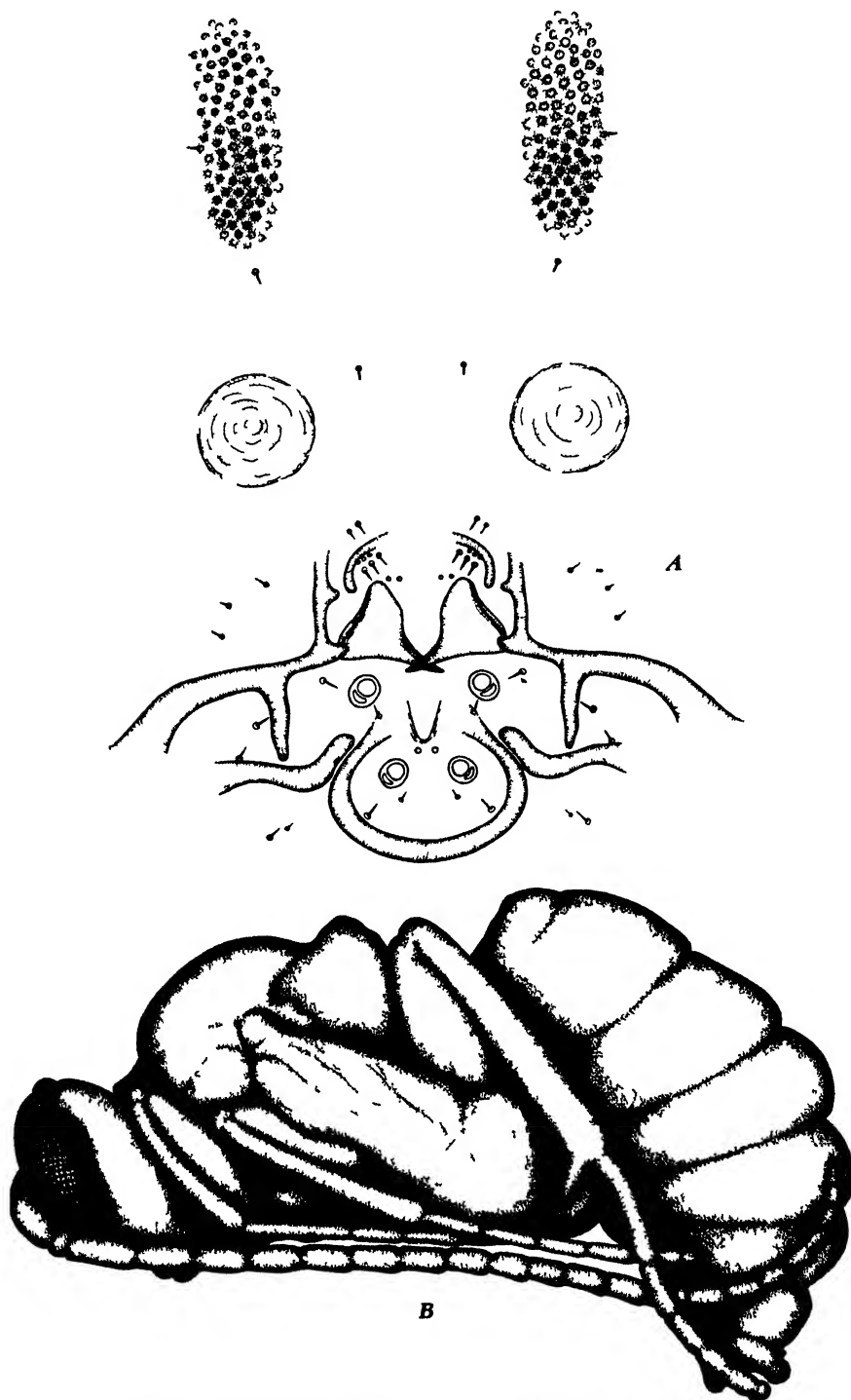
Fig. 36. *Chrysopoctonus patruelis* Cush A Facial structures of fifth instar larva.
B Male pupa.

Life Cycle.—According to laboratory observations, the life cycle is as follows:

Life cycle	Extremes	Averages
	days	*days*
Egg	1.0 –2.0..	1.25
First instar	1.0 –1.5..	1.25
Second instar	0.75–1.5..	1 0
Third instar	0.75–1.5..	1.0
Fourth instar	0.75–1.5..	1.0
Fifth instar	3.5 –6.0..	4 0
Prepupa	1.0 –2.0..	1 5
Pupa	5.0 –9.0..	6.0
Total	13.75–25.0..	17.0

Hemiteles tenellus (Say)

H. tenellus is one of the most common of all hyperparasites, having been reared from cocoons of a great variety of host insects (Cushman and Gahan, 1921). Although generally hyperparasitic, it often develops as a primary parasite; it is thus herein recorded from *C. californica.* Six species of *Chrysopa* and four of *Anamalochrysa* are listed as hosts; the localities are California, Virginia, and New York, in addition to Canada and the Hawaiian Islands.

At least six species of *Hemiteles* have been reared from chrysopid cocoons, the majority of them European. *H. tenellus* is indistinguishable taxonomically from the European *H. areator* (Muesebeck and Dohanian, 1927), also a *Chrysopa* parasite, and is often considered a subspecies or variety of *areator.* The former is thelyotokous, however, and males are unknown, whereas *H. areator* is represented by both sexes, and parthenogenetic reproduction is arrhenotokous.

Biological information exists on *H. areator* Panz. (Morris, Cameron and Jepson, 1937), *H. hemipterus* Fabr. (Salt, 1931), (Rosenberg, 1934), and *H. tenellus* (Proper, 1934), (Muesebeck and Dohanian, 1927). Because of the widespread occurrence and general importance of *H. tenellus,* further details are presented.

The Adult.—When unduly excited the adults were observed to feign death by rolling over with the legs flexed and remaining perfectly motionless for several seconds. Ovipositing females have lived 60 to 83 days.

Oviposition.—The oviposition procedure and paralyzation of the host as a primary parasite are essentially as described for *Chrysopoctonus patruelis.* Adults were frequently seen probing in the cotton vial plugs, and even empty *Chrysopa* cocoons are often investigated in this manner.

In order to observe the procedure more closely, host individuals were placed within glass capillary tubes closed at one end with cotton; a small piece of lens paper was glued over the opposite end. Females will oviposit readily through the paper cap, and the entire process may be followed under the binocular microscope. During the attack, a minute droplet of clear fluid accumulates on the outer surface of the lens paper. The host is generally completely inacti-

vated in from 2 to 20 minutes. Occasionally, however, paralysis is not induced even after repeated insertions of the ovipositor. As with *C. patruelis*, when once paralyzed the *Chrysopa* apparently never recovers, although it may remain alive for several days; the "preserved" condition may persist for as long as 14 days. Eggs are deposited only upon paralyzed hosts. A great many chrysopids are paralyzed without subsequent oviposition. The mortality from this factor alone often exceeds that attributable to parasitic development.

The egg is extruded at right angles to the ovipositor a short way up from the tip, so that as the appendage is withdrawn the egg adheres, by its ventral surface, to the inner wall of the cocoon. When *Isodromus* is the host, the egg is sometimes deposited thus, instead of within the melanized sheath; the newly emerged larva is then unable to reach its host.

Oviposition was as readily obtained upon *C. majuscula*, although adults never emerged. The newly hatched larvae frequently fed for a time, and several of them attained the second instar.

The host may be paralyzed and an egg laid at a single insertion of the ovipositor, or repeated insertions may be made over a much longer period before oviposition is effected. In the laboratory as many as 5 eggs were laid per host, although never more than a single larva matures.

Like many hyperparasites, *Hemiteles* feeds rather extensively at the puncture holes. This habit was much more pronounced as a secondary parasite. When *Chrysopa* pupae or prepupae were attacked, feeding was but rarely observed, and only upon those which had been rendered immobile. A delicate feeding tube is formed in the usual manner.

Several hemerobiid cocoons were offered in an attempt to secure oviposition. Owing to the open cocoon structure the mouth parts were applied directly to the pupa, or by bending the head and thorax downward the fluid was lapped up as the ovipositor moved up and down. The small pupae were soon partially deflated and no attempt was made at oviposition.

Muesebeck and Dohanian report a maximum of 76 eggs per female laid over a period of 51 days. The ovarioles are of the polytrophic type, each ovum being accompanied by a group of nutritive cells.

H. tenellus has been reared from nearly all of the primary parasites of *Chrysopa*, as well as from individuals of its own species.

Egg.—Both the ovarian and deposited eggs are similar to those of *Chrysopoctonus patruelis* (fig. 35, A and B), except that the longitudinal ridges are less pronounced. They averaged 0.78 mm. by 0.20 mm. Following an average incubation period of 36 to 48 hours, the larva emerges through the broad end of the egg.

Larvae.—There were also five instars in *H. tenellus;* the first and fifth stages only will be discussed.

First Instar.—The process of eclosion occupies 10 to 30 minutes. The dermal armature of minute papillae, most pronounced in the midlateral regions (fig. 37, A), probably assists in emergence.

The head capsule (fig. 37, B) is prominent and well sclerotized, bearing a pair of elongate, slender antennal papillae anteriorly. It averages 0.195 mm.

in width. Although nine pairs of spiracles are present in the primary larva, they are lacking in segments 2 and 3; the accessory structures accommodate those regions.

The completion of the first instar requires 1 to 2 days, the larva attaining a maximum size of 1.20 mm. by 0.32 mm. The mandibles (fig. 37, D) measure 0.035 mm. in length.
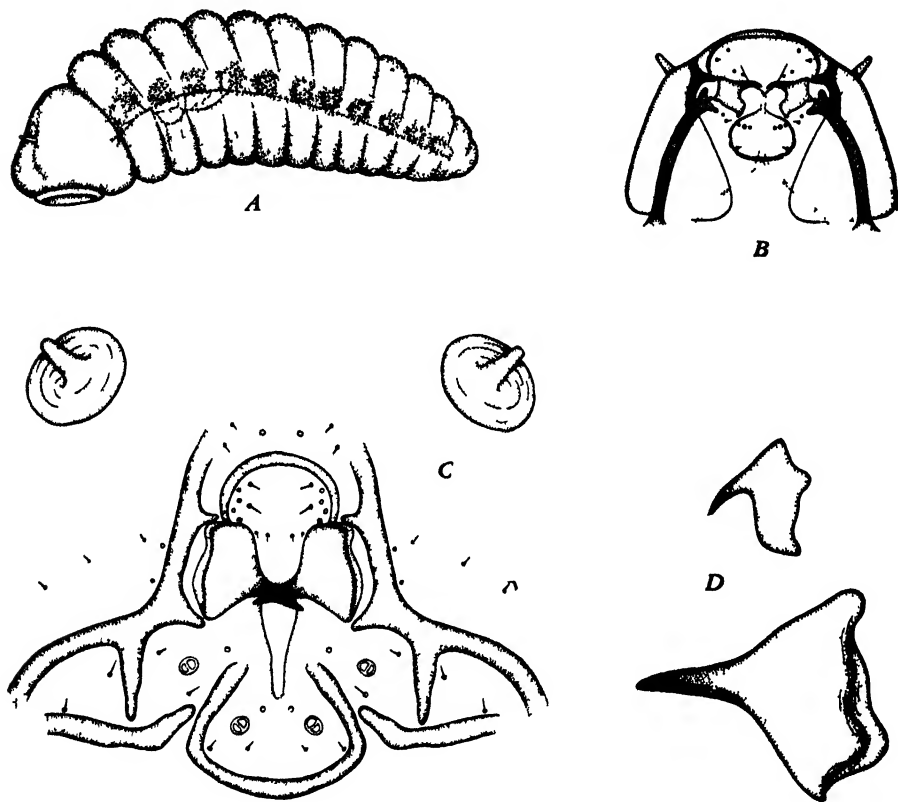
Fig. 37. *Hemiteles tenellus* (Say). A. First instar larva. B. Larval mouth parts of first instar. C. Same, fifth instar D. First and fifth instar mandibles.

Fifth Instar.—The mature larva (fig. 38, A) is similar in general to that of most ectoparasitic Ichneumonidae. The absence of dorsal cephalic tuberculate patches, together with the typical elongate larval antennae, will readily distinguish it from *C. patruelis*. In addition, the facial structures show certain morphological differences (fig. 37, C).

When full fed, average dimensions are approximately the same as for *C. patruelis*. The mandibles (fig. 37, D) measure 0.077 mm. in length. Spring and summer generation larvae require 4 to 9 days to complete the instar, and overwintering individuals pupate the following spring. The feeding period occupies 1 to 2 days, followed by a quiescent period of several days after which the delicate, papery cocoon is spun. It is invariably a complete silken envelope which may with care be separated from the walls of the *Chrysopa* cocoon.

Pupa —The pupa (fig. 38, B) hatches in 5 to 12 days; pupation generally occurs 10 to 16 days from oviposition. The exit hole is situated at or near one end of the host cocoon, and is similar to that of *C. patruelis.*

Parthenogenesis —A total of 131 females emerged from field-collected *C. californica* cocoons. Muesebeck and Dohanian (1927) have reared, over a pe-
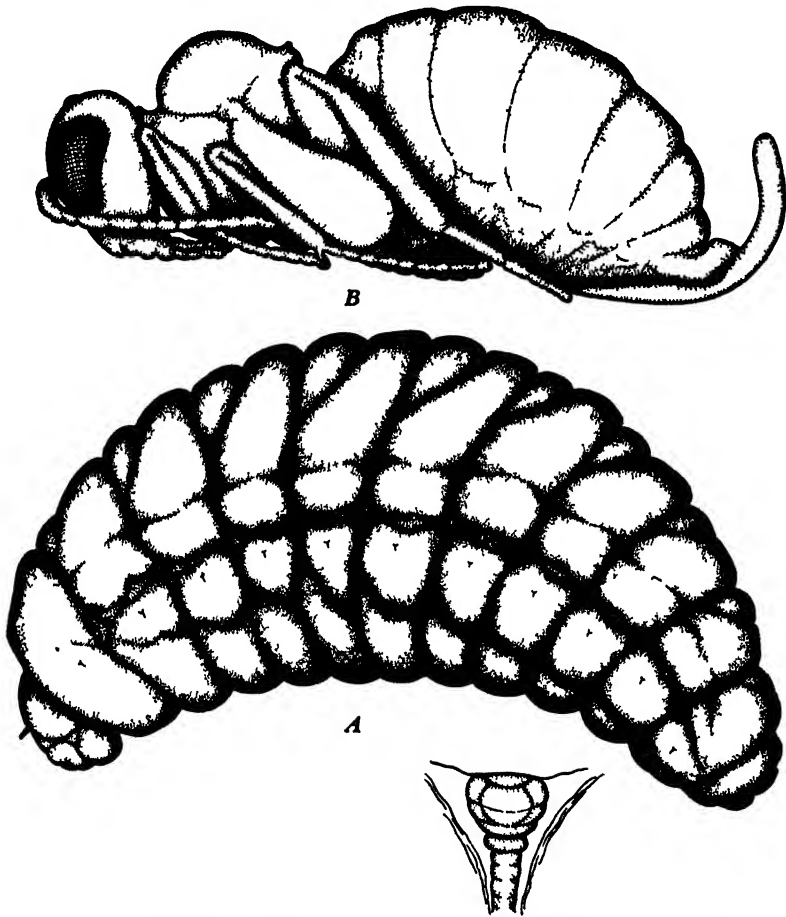
Fig 38 *Hemiteles tenellus* (Say) A Mature fifth instar larva showing enlarged spiracle B Pupa.

riod of three years, several pure lines of females through twelve generations, without obtaining a single male

Life Cycle.—A wide variation was shown in the number of annual generations in both laboratory and field-collected material Although the majority of spring and autumn generations was completed in 15 to 33 days, occasional individuals required as many as 120 days even during the summer, still others reared under identical conditions from the same females failed to emerge until the following year. Approximately one-fourth of those collected on orange during the summer overwintered.

The normal or usual life cycle is as follows:

Life cycle	Extremes	Averages
	days	*days*
Egg	1.5 – 3.0	2.0
First instar	1.0 – 2.0	1.5
Second instar	0.75– 1.5	1.0
Third instar	0.75– 1.5	1.0
Fourth instar	0.75– 1.5	1.0
Fifth instar	4.0 – 9.0	5.5
Prepupa	1.0 – 2.5	1.5
Pupa	5.0 –12.0	6.5
Total	14.75–33.0	20.0

Gelis sp.

This genus of the Ichneumonidae is composed of numerous species, both native and foreign, which appear to be largely hyperparasitic in habit. The females are apterous or subapterous, whereas the males are generally alate, although wingless forms have been described. Brues (1903) has monographed the North American species (formerly *Pezomachus*). The host relations are extremely varied; certain species are myrmecophilous in the nests of ants, some are predaceous in spider egg sacs, and a great many attack parasites of Lepidoptera within their cocoons. Other species have been reared from leaf miners and from a variety of other hosts.

According to R. A. Cushman, the present species does not agree with any other, but "... species of this genus are generally so lacking in distinctive characters that I hesitate to declare these specimens as representing a new species." This is the first record from the Chrysopidae, although Killington (1936) lists *Gelis ruficornis* Thbg. from a hemerobiid in England.

Only eight specimens of *Gelis* were bred from field-collected *Chrysopa* cocoons, all of them apterous females, and solely from *C. californica*. They apparently developed as primary parasites in each case, since the host cocoons showed no trace of an intermediate inhabitant. A single female also issued from a clerid cocoon (*Hydnocera* sp.).

Little biological information exists on members of this genus. Muesebeck and Dohanian (1927) have given notes on several species which parasitize *Apanteles melanoscelus*, and Proper (1934) records field parasitism in relation to certain Lepidoptera.

The Adult.—The antlike female cannot be confused with other *Chrysopa* parasites. It is similar in size to *H. tenellus* and variously marked with red and brownish black.

Oviposition.—In an effort to rear *Gelis* in the laboratory, numerous *C. californica* cocoons were offered, many of them containing pupae of the various primary parasites. Only one full-grown larva was obtained for study; it matured upon a chrysopid pupa. *Gelis* probably develops normally within spider egg sacs or clerid cocoons. Its occasional development upon a nonrelated host

would not be surprising; this characteristic is typical of a great many members of the genus.

Larva.—The ectoparasitic mature larva (fig. 39, A) is of the generalized ichneumonoid type. The conical larval antennae (fig. 39, B) are situated on prominent circular bases, and the labial and maxillary palpi (fig. 39, C) are distinct from those of *Chrysopoctonus* and *Hemiteles*. The larva measured 2.52 mm. by 1.17 mm The head capsule was approximately 0.46 mm. in breadth.

A complete silken envelope is spun within the *Chrysopa* cocoon similar to that of *H tenellus*
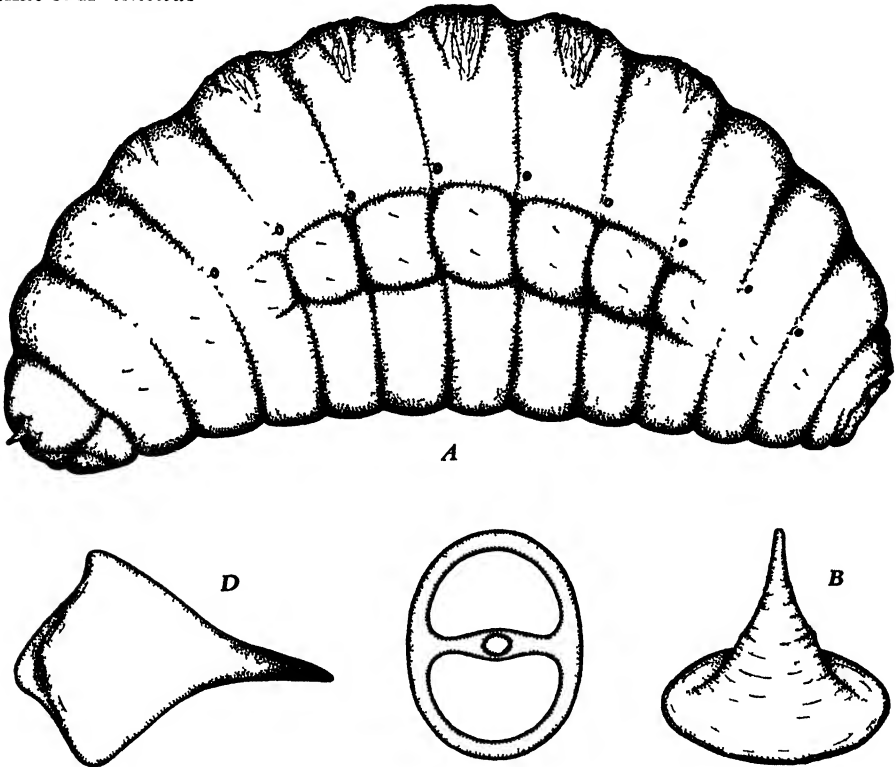
Fig 39 *Gelis* sp A Fifth (♀) instar larva. B Larval antenna of same.
C Labial palpus of same D Mandible of same.

CLERIDAE (Coleoptera)

Hydnocera scabra Lec , and *Hydnocera affiliata* Fall

Individuals of these two species[4] were commonly encountered beneath the burlap bands used for field studies of *Chrysopa* parasitism, where they were normally predaceous on codling moth Numerous *Chrysopa* cocoons of both species were also found riddled with holes by the predatory larvae Occasional cocoons were collected, however, containing mature clerid larvae or pupae with only a single, very small entrance hole. In order to ascertain whether development could be completed upon a single *Chrysopa*, a series of cocoons was individually infested with single newly hatched *Hydnocera* larvae. Adults of both *H. scabra*

[4] Determined by Dr E C Van Dyke

and *H. affiliata* emerged from a small porportion of the cocoons. A truly parasitic existence is thus possible, although predatism is the usual habit. The same conclusion was reached by Muesebeck and Dohanian (1927) with respect to *H. verticalis* Say which they obtained from cocoons of *Apanteles melanoscelus*
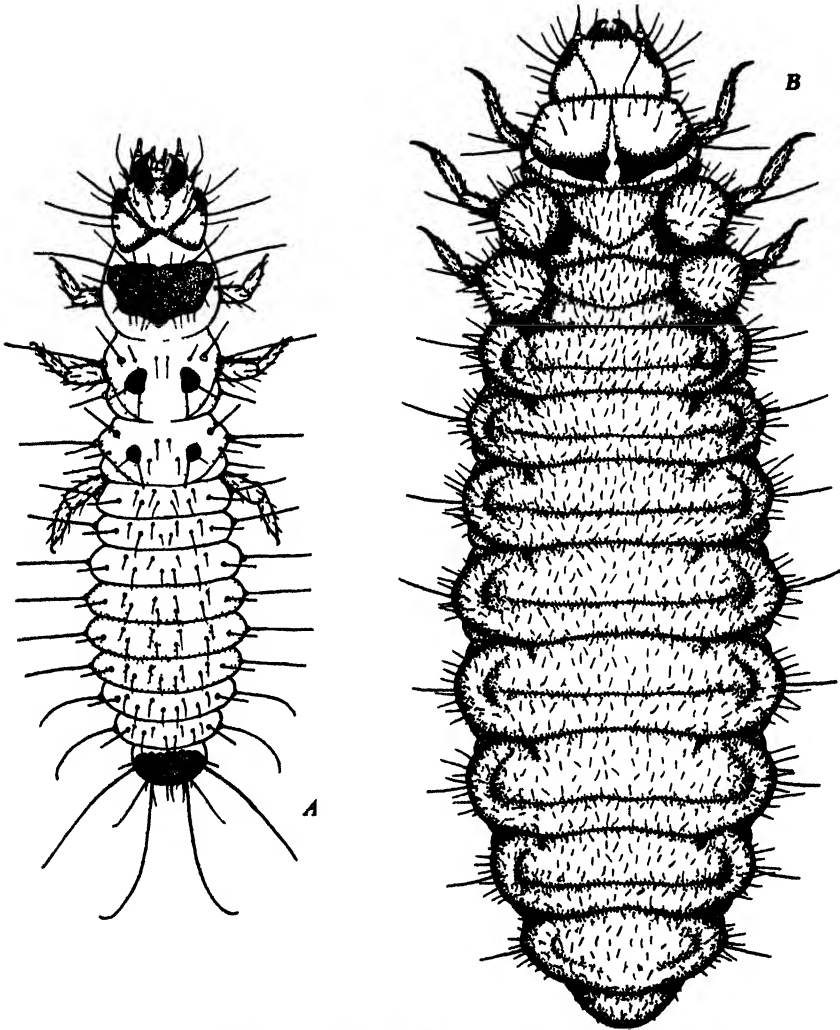
Fig. 40. *Hydnocera* spp. A. First-instar larva. B. Mature last-instar larva.

(Ratz.). The larvae of *Isohydnocera curtipennis* (Newmn.) (Sabrosky, 1934) are apparently parasitic in plant galls.

Two distinct types of first-instar larvae were observed in approximately equal numbers. One form was bright coral red in color, and the other (fig. 40, A) a dull white with a pale-pink band across the abdomen and with the meso and metathoracic segments faintly smoky in color. Nearly identical differences were noted in the mature larvae, the coral-colored form being shown in figure B. It is believed that figure A represents *H. scabra* and figure B, *H. affiliata*.

Many cocoons were also attacked by dermestid larvae (apparently *Anthrenus verbasci* Linn.) and the pupae partially or completely devoured. Larvae enclosed within gelatin capsules with *Chrysopa* cocoons soon riddled them completely and escaped through holes made in the capsules. Development was never parasitic as above. Howard (1897) records *Trogoderma* sp. as feeding upon live eggs of the Tussock moth and mentions a similar observation by Kuwert, the host being *Tenthredo lutea*.

No effort was made to secure quantitative data on the field occurrence of either clerids or dermestids.

DISCUSSION OF THE LITERATURE

A thorough perusal of the literature has uncovered a surprising number of records pertaining to parasites of the Chrysopidae. All three superfamilies of the parasitic Hymenoptera are abundantly represented, although the Diptera has only one species listed, a chironomid. In all, sixty-one species (several of them generic names only) are regarded as valid parasites of the Chrysopidae. *Brethesia* (two species) is also probably a genus of *Chrysopa* parasites, although no host records are available. Since the Hemerobiinae formerly included both the Chrysopidae and Hemerobiidae, such records are indefinite.

Of those families represented in the Chalcidoidea, there are four genera and ten species of encyrtids, one genus and species of Perilampidae, three genera and five species of the Eulophidae, two genera with two species in both the Pteromalidae and Eupelmidae, and the Trichogrammatidae is represented by two species of the type genus.

The Serphoidea contains only two families of recorded chrysopid parasites, the Scelionidae and Heloridae, the former with two species, and the latter with ten.

The Ichneumonoidea is approximately equal in number of species to the Chalcidoidea; twenty-one ichneumonids are listed belonging to eight genera, whereas the Braconidae is represented by three species in a single genus. In addition, there are two clerids (one genus) and one chironomid.

It is noteworthy that one genus in each of the three superfamilies, namely, *Isodromus*, *Helorus*, and *Chrysopoctonus*, is apparently composed of species which parasitize only members of the Chrysopidae.

All stages of the Chrysopidae are attacked. With the exception of five species of egg parasites (families Encyrtidae, Trichogrammatidae, and Scelionidae) and one adult parasite (family Chironomidae), all parasitize either larvae, prepupae, or pupae, and so far as is known they all normally issue from the host cocoon. Only one species (*Perilampus chrysopae*) has been shown to develop solely upon the pupa; the others generally complete their larval development upon or within the prepupa, utilizing the host cocoon as protection during the pupal stage. Those species which oviposit through the *Chrysopa* cocoon as primary parasites are able to mature upon either stage. Four of the investigated species were found to be invariably endoparasitic and ten were ectoparasitic. Larval development in the hyperparasites was ectophagous in all but a single species.

TABLE 1

THE RECORDED PARASITES OF THE CHRYSOPIDAE

Parasite	Host	Locality	Reference
CHALCIDOIDEA			
(1) ENCYRTIDAE			
1. Isodromus iceryae How.	Chrysopa californica Coq.	California	F. R. Cole, 1933
	Chrysopa californica Coq.	California	E. O. Essig, 1926
	Chrysopa californica Coq.	California	Reared by author 1935–1937
	Chrysopa sp.	California	P. H. Timberlake, 1919
	Sympherobius angustus Banks*	California	E. O. Essig, 1913
	Sympherobius angustus Banks*	California	F. R. Cole, 1933
	Sympherobius californicus Banks*	California	C. P. Clausen, 1915
	Chrysopa rufilabris Burm. (?)	South Carolina	McGregor and McDonough, 1917
"(Paratameostigma nigriaxillae Gir.)"	Chrysopa rufilabris Burm. (?)	Kansas	R. C. Smith, 1934
	Chrysopa lateralis Guer.	Florida	R. C. Smith, 1922
	Chrysopa lateralis Guer.	Florida	M. Rühl, 1925†
	Chrysopa sp.	Florida	
		Missouri	
		Washington, D.C.	
		Maryland	
"(Paratameostigma nigriaxillae Gir.)"	Chrysopa sp.	Mexico	L. O. Howard, 1891
	Eremochrysa punctinervis (McLach.)	California	P. H. Timberlake, 1919
			Reared by author; parasitized in laboratory
2. Isodromus niger Ashm.	Chrysopa majuscula Banks	California	Reared by author 1935–1937
	Chrysopa californica Coq.*	California	F. R. Cole, 1933
	Chrysopa sp.	California	P. H. Timberlake, 1919
	Sympherobius angustus Banks*	California	F. R. Cole, 1933
	"Hemerobiid cocoon"*	California	P. H. Timberlake, 1919
	Chrysopa oculata Say	Wisconsin	C. L. Fluke, 1929
	Chrysopa sp.	Washington, D.C.	W. H. Ashmead, 1900
	Chrysopa sp.	Utah, Massachusetts, Formosa Island	P. H. Timberlake, 1919

Parasite	Host (Chrysopa)	Locality	Authority
3. *Isodromus puncticeps* (How.)	*Chrysopa* sp.	Spain	R. G. Mercet, 1921
"(*I. chrysopae*)"	*Chrysopa* sp.	California	P. H. Timberlake, 1919
	Chrysopa sp.	Virginia, Florida, and Washington, D.C.	W. H. Ashmead, 1900
4. *Isodromus atriventris* Ashm.	*Chrysopa* sp.		N. Banks, 1903
	Chrysopa lateralis Guer.	Florida	R. C. Smith, 1922
	Chrysopa lateralis Guer.		M. Rühl, 1926†
	Chrysopa sp.	Virginia, Canada, and Massachusetts	P. H. Timberlake, 1919
5. *Isodromus flaviceps* (Dalm.)		Sweden	P. H. Timberlake, 1919
6. *Isodromus axillaris* Timb.	*Chrysopa boninensis* Okam.	Japan	T. Ishii, 1932†
		China	P. H. Timberlake, 1919
7. *Isodromus vinulus* (Dalm.)	*Chrysopa microphya* McLach.	Hawaii	O. H. Swezey, 1936
	Chrysopa sp.	Spain	R. G. Mercet, 1921
		Sweden	P. H. Timberlake, 1919
8. *Brethesia abnormicornis* (Gir.) "(*Isodromus abnormicornis*)" (Probably *Chrysopa* parasite)		South America	P. H. Timberlake, 1919
9. *Brethesia latifrons* Timb.		South Carolina	P. H. Timberlake, 1919
10. *Chrysopophagus compressicornis* Ashm.	*Chrysopa ruflabris* Burm.	South Carolina	McGregor and McDonough, 1917
	Chrysopa attenuata Walk.	Mississippi	W. H. Ashmead, 1894
	Chrysopa spp.		N. Banks, 1903
	Chrysopa californica Coq. (hyperparasitic)	California	Reared by author 1935–1937
	Chrysopa mijuscula Banks (hyperparasitic)	California	Reared by author 1935–1937
11. *Chrysopophilus compressiventris* Timb.	*Chrysopa* sp.	Panama	P. H. Timberlake, 1925
12. *Ooencyrtus chrysopae* Cwfd.	*Chrysopa* sp. (eggs)	Trinidad	J. C. Crawford, 1913

* Host record questionable.
† Original reference not seen.
‡ Smulyan records the following localities: Maine, New Hampshire, Washington, D.C., Massachusetts, Vermont, Rhode Island, New York, New Jersey, Pennsylvania, Illinois, Maryland, North Carolina, South Carolina, Michigan, Indiana, Oklahoma, Alabama, Virginia, Wisconsin, Mississippi, South Dakota, Kansas, Montana, Wyoming, Colorado, Texas, Idaho, Nevada, Washington, Oregon, California, and Canada.

TABLE 1—*Continued*

Parasite	Host	Locality	Reference
CHALCILOIDEA—*Continued*			
(2) PERILAMPIDAE			
13. *Perilampus chrysopae* Cwfd.	*Chrysopa californica* Coq.	California	E. O. Essig, 1926
	Chrysopa californica Coq.	California	Reared by author 1935–1937
(incl. var. *laevicephalus* Cwfd.)	*Chrysopa californica* Coq.	California	J. C. Crawford, 1916
	Sympherobius angustus Banks*	California	E. O. Essig, 1926
	Chrysopa rufilabris Burm.	South Carolina	McGregor and McDonough, 1917
	Chrysopa rufilabris Burm.	Virginia and Ohio	R. C. Smith, 1922
	Chrysopa rufilabris Burm.	Canada	M. Rühl, 1925†
	Chrysopa sp.	30 states, Washington D.C., and Canada‡	W. L. Putman, 1937
	"ex *Chrysopa* spp."		
Perilampus sp.	*Chrysopa oculata* Say (?)	Virginia	M. T. Smulyan, 1936
(probably *P. chrysopae*)			R. C. Smith, 1922
Perilampus hyalinus Say	*Chrysopa* sp.	California	H. S. Smith, 1912
	Chrysopa sp.	Mississippi	W. H. Ashmead, 1904
	Chrysopa attenuata Wlk.	Mississippi	W. H. Ashmead, 1895
(probably *P. chrysopae*)	*Chrysopa* sp.		N. Banks, 1903
(3) EULOPHIDAE			
14. *Tetrastichus chrysopae* Cwfd.	*Chrysopa californica* Coq.	California	F. R. Cole, 1933
	Chrysopa californica Coq.	California	Reared by author 1935–1937
("*Geniocerus chrysopae*")	*Chrysopa rufilabris* Burm.	South Carolina	McGregor and McDonough, 1917
	Chrysopa rufilabris Burm.	Virginia and Ohio	R. C. Smith, 1922
	Chrysopa rufilabris Burm.		M. Rühl, 1925†
15. *Tetrastichus pubescens* Nees.	*Chrysopa* sp.	Russia	M. Nikol'skaya, 1934
16. *Tetrastichus blepyri* Ashm.	*Chrysopa californica* Coq. (hyperparasitic on *Pachyneuron californicum*)	California	F. R. Cole, 1933
Tetrastichus sp.	*Chrysopa* sp.	Louisiana	L. O. Howard, 1892
(probably *T. chrysopae*)			
17. *Syntomosphyrum orgyiae* Ashm.	*Chrysopa* spp.		N. Banks, 1903
18. *Horismenus* sp.	*C. lateralis* Guer.	Florida	R. C. Smith, 1922

(4) PTEROMALIDAE

19. *Pachyneuron californicum* Gir.		
Chrysopa californica Coq.	California	F. R. Cole, 1933
Chrysopa californica Coq. (hyperparasitic)	California	Reared by author 1935–1937
Chrysopa majuscula Banks (hyperparasitic)	California	Reared by author 1935–1937
20. *Dibrachys cavus* Wlk. (*boucheanus* Ratz.)		
Chrysopa californica Coq. (both primary and secondary)	California	Reared by author 1935–1937
Chrysopa majuscula Banks (both primary and secondary)	California	Reared by author 1935–1937
Chrysopa rufilabris Burm. (both primary and secondary)	Wisconsin	R. C. Smith, 1922
Chrysopa rufilabris Burm. (hyperparasitic)		
Chrysopa sp.	Russia	M. Rühl, 1924† M. Nikol'skaya, 1934

(5) EUPELMIDAE

21. *Eupelmus chrysopinus* Perk.		
Anomalochrysa gayi Perk.	Hawaiian Islands	O. H. Swezey, 1936
Anomalochrysa deceptor Perk.		
Anomalochrysa raphidioides Perk.		
Anomalochrysa proteus Perk.		
22. *Arachnophaga picea* How. *Chrysopa californica* Coq.	California	Reared by author 1935–1937
***Arachnophaga* sp. (probably *A. picea*)** *Chrysopa lateralis* Guer.	Florida	R. C. Smith, 1922

(6) TRICHOGRAMMATIDAE

23. *Trichogramma minutum* Riley		
Chrysopa oculata Say (eggs)	Canada	L. J. Briand, 1931
Chrysopa albicornis Fitch (eggs)	Canada	L. J. Briand, 1931
Anomalochrysa gayi Perk.		
Anomalochrysa deceptor Perk.		
Anomalochrysa raphidioides Perk.	Hawaiian Islands	O. H. Swezey, 1936
Anomalochrysa proteus Perk. (eggs)		
Chrysopa sp. (eggs)	Canada	W. L. Putman, 1937
Chrysopa sp. (eggs)		R. C. Smith, 1922
24. *Trichogramma embryophagum* (Htg.) *Chrysopa californica* Coq.	California	Reared by author 1935–1937

TABLE 1—*Continued*

Parasite	Host	Locality	Reference
SERPHOIDEA			
(7) HELORIDAE			
25. *Helorus paradoxus* Prov.	*Chrysopa majuscula* Banks	California	Reared by author 1935–1937
	Chrysopa sp.	Minnesota	F. L. Washburn, 1918
	Chrysopa sp.	Connecticut	H. L. Viereck, 1916
	Chrysopa sp.	Massachusetts.	G. Dimmock, 1898
		Indiana	B. E. Montgomery, 1933
		Montana and Canada	W. H. Ashmead, 1893
	Chrysopa sp.	New York	R. C. Smith, 1922
26. *Helorus chrysopae*	*Chrysopa oculata* (?) Say		M. Rühl, 1926†
(*H. paradoxus*?)	*Chrysopa oculata* (?) Say		
27. *Helorus corruscus* Hal.	*Chrysopa flava* Scop.	England	C. L. Withycombe, 1923
	Chrysopa ciliata Wesm.	England	F. J. Killington, 1933
	Chrysopa ventralis Curt.	Germany and England	C. L. Withycombe, 1923
28. *Helorus rugosus* Thomas.	*Chrysopa septempunctata* Wesm.	England	C. G. de Dalla Torre, 1898
		Sweden	C. G. Morley, 1935†
29. *Helorus ruficornis* Fst.	*Chrysopa* spp.	England	C. G. de Dalla Torre, 1898
		Germany	F. J. Killington, 1933
30. *Helorus anomalipes* Panz.	*Chrysopa flava* (?) Scop.	France	J. Feytaud, 1913†
	Chrysopa spp.	France	R. Regnier, 1923
	Chrysopa vulgaris Wesm.	Europe (throughout)	C. G. de Dalla Torre, 1898
31. *Helorus ater* Jur.	"Hemerobiinae"	"Europe"	L. O. Howard, 1891
	Chrysopa (?) sp.	"Europe"	C. G. A. Brischke, 1882†
		Switzerland	C. G. de Dalla Torre, 1898
32. *Helorus flavipes* Kief.		France	J. J. Kieffer, 1907
33. *Helorus nigripes* Fst.		Sweden and Germany	C. G. de Dalla Torre, 1898
34. *Helorus striolatus* Cam.		India	P. Cameron, 1906†
35. *Helorus brethesi* Oglb.		South America	D. A. Oglobin, 1928†
Helorus sp. (probably *H. paradoxus*)	*Chrysopa rufilabris* Burm.	South Carolina	McGregor and McDonough, 1917

Parasite	Host	Locality	Authority
(8) SCELIONIDAE			
36. *Telenomus chrysopae* Ashm.	*Chrysopa rufilabris* Burm.	South Carolina	McGregor and McDonough, 1917
	Chrysopa sp.	Washington, D.C.	W. H. Ashmead, 1893
	Chrysopa spp.	Connecticut	H. L. Viereck, 1916
	Chrysopa spp.		N. Banks, 1903
	Chrysopa spp.	Russia	I. V. Vassiliev, 1915†
37. *Telenomus acrobates* Giard	*Chrysopa vulgaris* Wesm.	France	M. Rühl, 1921†
	Chrysopa sp.	France	R. Regnier, 1923†
	Chrysopa flavifrons Br.	France	R. Regnier, 1923†
	Chrysopa sp.	Germany	J. L. Lacroix, 1923†
	Chrysopa carnea Steph.	"Europe"	H. Bischof, 1923†
	Chrysopa sp.	France	J. Feytaud, 1913†
	Chrysopa perla (Linn.)	France	A. Giard, 1895
Telenomus sp.		United States (probably Europe)	L. O. Howard, 1888
	"*Chrysopa* or *Hemerobius*"	United States	L. O. Howard, 1891
	Chrysopa sp.	Japan	C. P. Clausen (unpublished correspondence)
ICHNEUMONOIDEA			
(9) ICHNEUMONIDAE			
38. *Hemeteles tenellus* (Say)	*Chrysopa californica* Coq.	California	Reared by author 1935–1937
	Chrysopa nigricornis Burm.	New York	R. C. Smith, 1922
	Chrysopa rufilabris Burm.	Virginia	R. C. Smith, 1922
	Chrysopa rufilabris Burm. and *C. plorabunda* Fitch (hyperparasitic on *Chrysopoctonus rileyi*)		
	Chrysopa microphya McL.	Canada	W. L. Putman, 1937
	Anomalochrysa guyi Perk., *deceptor* Perk., *Broteus* Perk., and *raphidioides* Perk.	Hawaiian Islands	O. H. Swezey, 1936
	Chrysopa rufilabris Burm. and *C. oculata* Say	Hawaiian Islands	O. H. Swezey, 1936
			M. Rühl, 1926†

TABLE 1—Continued

Parasite	Host	Locality	Reference
ICHNEUMONOIDEA—Continued			
(9) ICHNEUMONIDAE—Continued			
39. Hemiteles aestivalis Grav.	Chrysopa perla L.	England	F. J. Killington, 1933
	Chrysopa perla L.	"Europe"	Kirchner, 1867†
	Chrysopa perla L. and Chrysopa sp.	"Europe"	J. B. Bridgman, 1883
	Chrysopa flava Scop.	England	F. J. Killington, 1933
	Chrysopa vulgaris Wesm.	France	C. L. Withycombe, 1923
	Chrysopa prasina Burm.	Italy	R. Regnier, 1923†
	Chrysopa carnea Steph.	"Europe"	A. Goidanich, 1931†
	Chrysopa carnea Steph.	"Europe"	J. Feytaud, 1913†
	"Hemerobiinae" (hyperparasitic)	"Europe"	R. Regnier, 1923†
	Chrysopa sp.	Poland	L. O. Howard, 1891
40. Hemiteles castaneus Tasch.	Chrysopa sp.	Germany (?)	R. Bledowski and M. K. Krainska, 1925†
(var. bridgmani)	"Hemerobiinae" (hyperparasitic)	"Europe"	C. G. A. Brischke, 1882†
41. Hemiteles areator Pz.	Chrysopa sp.	Austria	L. O. Howard, 1891
	Chrysopa sp.	Poland	F. Schonwiese, 1934
	"Hemerobiinae" (hyperparasitic)	"Europe"	R. Bledowski and M. K. Krainska, 1925†
	Chrysopa (?) sp.	Germany (?)	L. O. Howard, 1891
42. Hemiteles rufiventris Riley	"Hemerobiinae" (hyperparasitic)	United States	C. G. A. Brischke, 1882†
43. Hemiteles hemerobiicola Ashm.	"Hemerobiinae" (hyperparasitic)	United States	L. O. Howard, 1891
44. Hemiteles limbatus Grav.	"Hemerobiinae" (hyperparasitic)	"Europe"	L. O. Howard, 1891
45. Hemiteles (Charitopes) chrysopae Br.	Chrysopa sp.	Germany (?)	C. G. A. Brischke, 1882†
	Chrysopa sp.	Germany	C. G. de Dalla Torre, 1902
		Germany	C. G. A. Brischke, 1890†
46. Hemiteles chrysopae Uch. "(egg[?])"	Chrysopa septempunctata var. cognata M'L.	Japan	T. Uchida, 1933†
Hemiteles (Perilitus) sp.	Chrysopa spp.	Canada	W. L. Putman, 1932
	Chrysopa oculata Say	Florida	H. G. Hubbard, 1885
	"Hemerobiinae" (hyperparasitic)	"Europe"	L. O. Howard, 1891
	Chrysopa (?) sp.	Germany (?)	C. G. A. Brischke, 1882†

Parasite	Host	Locality	Authority
47. *Chrysopoctonus patruelis* Cushm.	*Chrysopa californica* Coq.	California	Reared by author 1935–1937
	Chrysopa californica Coq.	California	E. O. Essig, 1926
	Chrysopa californica Coq.	California	F. R. Cole, 1933
	Chrysopa sp.	California	R. A. Cushman, 1919
48. *Chrysopoctonus rileyi* (Ashm.)	*Chrysopa* sp.	Pennsylvania	R. A. Cushman, 1919
	Chrysopa nigricornis Burm., *C. rufilabris* Burm., and *C. plorabunda* Fitch	Canada	W. L. Putman, 1937
("*H. euryptychiae*")	"*Hemerobius*"	Missouri	W. H. Ashmead, 1896
("*Ouacustes cressoniformis*")		Connecticut	H. L. Viereck, 1916
("*Hemiteles hemerobii*")		Michigan	W. H. Ashmead, 1890
49. *Chrysopoctonus bicolor* Cushm.	*Chrysopa lateralis* Guer.	Florida	R. A. Cushman, 1924
	Chrysopa lateralis Guer.		M. Rühl, 1927†
50. *Chrysopoctonus atriceps* Ashm.	*Chrysopa oculata* Say	Mississippi	W. H. Ashmead, 1894
("*Oeducustes atriceps*")	*Chrysopa oculata* Say	Missouri	C. G. de Dalla Torre, 1902
("*Orthizema atriceps*")	*Chrysopa rufilabris* Burm.	South Carolina	McGregor and McDonough, 1917
51. *Chrysopoctonus chrysopae* (Ashm.)	*Chrysopa oculata* Say	Missouri	N. Banks, 1903
("*Otacustes chrysopae*")	*Chrysopa oculata* Say	Mississippi	C. G. de Dalla Torre, 1902
52. *Brachycyrtus navaii* (Ashm.)	*Chrysopa* sp.	Philippine Islands	W. H. Ashmead, 1894
53. *Porizon perlae* Gir.	*Chrysopa perla* L.	"Europe"	R. A. Cushman, 1936
54. *Mesochorus* (?) *chrysopae*.	"Hemerobiinae" (hyperparasitic)	"U.S.A."	L. O. Howard, 1888
55. *Mesochorus pectoralis* Ratz.	*Chrysopa* sp.	England	L. O. Howard, 1891
56. *Brachycephalus ruficollis* Grav.	*Chrysopa* sp.	England	C. L. Withycombe, 1923
		England	Massee, Thomas, and Hey, 1935†
57. *Phaeogenes* sp.	*Chrysopa carnea* Steph.	England	A. E. Cameron, 1913†
58. *Gelis* sp.	*Chrysopa californica* Coq.	California	Reared by author 1935–1937
(10) BRACONIDAE			
59. *Microgaster perlae* Doum.	*Chrysopa vulgaris* Wesm.	France	R. Regnier, 1923†
	Chrysopa carnea Steph.	France	A. J. L. Doumerc, 1855
60. *Microgaster ater* Ratz.	"Hemerobiinae"	"Europe"	L. O. Howard, 1891
61. *Microgaster ultor.*	*Chrysopa* (?) sp.* (probably ex hemerobiid)	Germany (?)	C. G. A. Brischke, 1882†
Microgaster sp.	*Chrysopa perla* L.	"Europe"	L. O. Howard, 1888

TABLE 1—*Concluded*

Parasite	Host	Locality	Reference
CYNIPOIDEA			
(11) FIGITIDAE			
62. *Aegalips clarimontis* Kief..........	*Chrysopa californica* Coq. *	California	F. R. Cole, 1933
		"Europe"	L. O. Howard, 1891
Anacharis ensifera Walk..........	"Hemerobiinae"	Germany (?)	C. G. A. Brischke, 1882†
CHIRONOMIDAE (DIPTERA)			
(1) *Pseudoculicoides eques* Johann..........	*Chrysopa oculata* Say,	New York	R. C. Smith, 1922
	C. chi Fitch,		
	C. nigricornis Burm., and		
	Meleoma signoretti Fitch..........		
(on wings of adult Chrysopidae) "Cecidomyidae?"	*Chrysopa chi* Fitch..........	New York and New Hampshire	N. Banks, 1903
	Chrysopa flavifrons Br., and	England	F. W. Edwards, 1932
	C. perla Linn..........		
CLERIDAE (COLEOPTERA)			
(1) *Hydnocera scabra* Le C..........	*Chrysopa californica* Coq..........	California	Reared by author 1935–1937
Hydnocera affiliata Fall..........	*Chrysopa californica*..........	California	Reared by author 1935–1937

THE FIELD ASPECT OF PARASITISM

In common with most general predators, the Chrysopidae are of secondary importance in the biological control of insect pests. The abundance of *Chrysopa* is apparently dependent upon host density, in that the predator is unable to increase appreciably until the prey have attained large numbers. This abundance results in economic damage before control can be effected. Indications are, however, that the attack on late summer generations of aphids, following the peak of infestation, may be beneficial through the reduction in individuals which will deposit overwintering eggs.

Essentially the same type of fluctuation was found among the parasites of *Chrysopa*. The rise and fall of parasitism generally follows closely that of the host, depending somewhat upon the locality, host plant, and relative abundance of the two species of *Chrysopa*. Without exception those orchards which continually maintained the greatest number of chrysopids also exhibited the highest average parasitism, and vice versa. There are also indications that the overwintering parasites, if sufficiently abundant, may somewhat retard the build-up of chrysopids the following spring, although parasitism in general, even though at times approaching 100 per cent, seems to have relatively little effect upon the average density of *Chrysopa* populations. The abundance of prey largely determines the numbers of *Chrysopa*, and the degree of parasitism is, in turn, obviously a function of host density.

Certain interesting variations have been noted in both the host and parasite fauna according to the host plant from which they were collected. The following condensed summaries present this data from a comparative standpoint.

On Walnut.—The most numerous and extensive collections were made on commercial plantings of English walnut over a period of approximately two years. A total of 7,586 *Chrysopa* cocoons was thus obtained from banded trees, representing 52 individual collections in seven localities from the counties of Los Angeles, Orange, Riverside, Ventura, and San Diego. All collections, except for one, were made at more or less regular intervals from the same bands at each station.

Parasites	No. cocoons parasitized	Per cent total parasites
Isodromus iceryae	1,339	38.8
Perilampus chrysopae	1,145	33.2
Isodromus niger	313	9.1
Chrysopophagus compressicornis	234	6.8
Chrysopoctonus patruelis	132	3.8
Dibrachys cavus	127	3.7
Tetrastichus chrysopae	100	2.9
Pachyneuron californicum	19	0.6
Arachnophaga picea	18	0.5
Helorus paradoxus	15	0.4
Hemiteles tenellus	4	0.1
Gelis sp.	1	0.03
	3,447	

Chrysopidae	Cocoons collected		Average number per band	Per cent parasitism	
	Number	Per cent		Primary	Secondary
Chrysopa californica............	5,677	74.8	6.0	75.9	30.8
Chrysopa majuscula............	1,909	25.2	2.0	24.3	1.6
	7,586		8.0		

Of the twelve species reared, *Isodromus iceryae* and *Perilampus chrysopae* were by far the most abundant parasites of *Chrysopa californica*, being obtained in nearly equal proportions, whereas *Isodromus niger* was most frequently bred from *C. majuscula*. It is noteworthy that the total primary parasitism of both species is almost exactly proportional to the host density as represented by the number of cocoons collected and the number per band.

C. californica becomes most abundant during midsummer, whereas with *C. majuscula* the overwintering emergents produce a spring and early summer peak which generally subsides during midsummer, being followed by a second and more pronounced autumn peak. The walnut aphid, *Chromaphis juglandicola* Kalt., constitutes almost the only prey of the chrysopids. Very few other arthropods suitable for food occurred.

Although *Hemiteles tenellus* and *Dibrachys cavus* will also develop as primary parasites, hyperparasitism is the rule; since it was impossible to investigate each case separately, these species were considered solely hyperparasitic.

On Apple.—A total of 1,174 *Chrysopa* cocoons was collected with apple as the host plant. There were three localities in Los Angeles and San Bernardino counties from which 17 collections were made.

Parasites	No. cocoons parasitised	Per cent total parasites
Isodromus niger...	202	67.3
Perilampus chrysopae....................................	50	16.7
Isodromus iceryae.......................................	23	7.7
Helorus paradoxus.......................................	12	4.0
Gelis sp..	7	2.3
Dibrachys cavus...	4	1.3
Chrysopoctonus patruelis................................	2	0.7
	300	

Chrysopidae	Cocoons collected		Average number per band	Per cent parasitism	
	Number	Per cent		Primary	Secondary
Chrysopa californica............	357	30.4	1.6	27.5	1.8
Chrysopa majuscula............	817	69.6	3.7	32.6	0.0
	1,174		5.3		

Here *Chrysopa majuscula* was invariably the most common species. Its prey consisted mainly of the woolly apple aphid, *Eriosoma lanigerum* (Haus.), together with smaller numbers of various other aphids. *C. majuscula* shows a decided preference for the woolly apple aphid, whereas *C. californica* fed mainly on the smaller green aphids. The concentrated attack of the Coccinellidae, Syrphidae, and Chrysopidae generally reduced the woolly aphis to negligible numbers by late June or early July, and the advent of hot weather seemed to limit the other aphids. Consequently, the collections herein recorded were made mostly from May to July. Almost no chrysopids were to be found during the remainder of the year.

Since *C. majuscula* was the dominant host species, *Isodromus niger* was the most abundant parasite encountered. *Perilampus chrysopae* and *I. iceryae* were again the most important parasites of *C. californica*, although the former was reared more than twice as frequently as the latter. *Helorus paradoxus*, apparently always an uncommon species, was more abundant on apple in proportion to its host than on any other host plant. The decrease in hyperparasitism was probably due to a lower average host density and to the much shorter period of chrysopid activity.

On Orange.—Various citrus-infesting mealybugs (*Pseudococcus* spp.) occasionally become sufficiently abundant to support large numbers of chrysopids before being controlled by other natural enemies. Several such infestations were found and the trees banded in the usual manner. A total of 2,052 *Chrysopa* cocoons was thus collected from three neighboring orange orchards in Los Angeles County.

Parasites	No. cocoons parasitized	Per cent total parasites
Isodromus iceryae	213	40.6
Hemiteles tenellus	127	24.2
Perilampus chrysopae	101	19.3
Chrysopoctonus patruelis	66	12.6
Dibrachys cavus	11	2.1
Isodromus niger	5	1.0
Tetrastichus chrysopae	1	0.2
	524	

Chrysopidae	Cocoons collected		Average number per band	Per cent parasitism	
	Number	Per cent		Primary	Secondary
Chrysopa californica	2,019	98.4	7.0	37.3	9.1
Chrysopa majuscula	33	1.6	0.1	22.7	0.0
	2,052		7.1		

The scarcity of *Chrysopa majuscula* is rather striking. Although an arboreal species, it occurred only sparingly on citrus. The parasitism recorded is probably not very significant because of the few individuals collected.

With respect to *C. californica*, the unusual abundance of *Hemiteles tenellus* is noteworthy. After numerous examinations and dissections of material, it is believed that primary parasitism by that species was of more frequent occurrence than usual. An arbitrary division was therefore made, one-half of the species being considered as primary parasites and the other half as hyperparasites. The above figures were computed on this basis. Although *Isodromus iceryae* and *Perilampus chrysopae* were again the most important species, the former was over twice as abundant, thus exactly reversing the ratio on apple. The ichneumonid *Chrysopoctonus patruelis* was also relatively more abundant on citrus than on any other host plant.

In order to ascertain whether there was any significant difference in parasitism as between those cocoons beneath bands and those spun among the foliage, separate collections were made from foliage. The latter were found to exhibit a slightly higher average parasitism. It is also believed that chrysopid populations on citrus are considerably higher than indicated by band collections because of the dense foliage cover. Consequently, a much smaller percentage of hosts is probably attracted to the bands than on either walnut or apple.

On Cotton.—The single collection on cotton was made by Mr. Gordon L. Smith in December, 1937, from cotton-gin trash in the Arvin area of the San Joaquin Valley. From these cocoons I reared the following species.

Parasites	No. cocoons parasitized	Per cent total parasites
Tetrastichus chrysopae	212	72.1
Perilampus chrysopae	68	23.1
Chrysopoctonus patruelis	14	4.8
	294	

Chrysopidae	Cocoons collected		Per cent parasitism	
	Number	Per cent	Primary	Secondary
Chrysopa californica	1,683	98.2	69.6	0
Chrysopa majuscula	31	1.8	0.0	0
	1,714			

As with orange as host plant, *Chrysopa majuscula* was very scarce. No parasites issued from the 31 cocoons collected.

C. californica, however, was parasitized to the extent of 69.6 per cent, nearly three-fourths of which was due to *Tetrastichus chrysopae*. The previous high was 2.9 per cent on walnut. It seems that *Tetrastichus* is particularly well adapted to the conditions under which cotton is grown; the species was

originally described from cotton in South Carolina. *Isodromus iceryae*, generally the most abundant parasite of *C. californica*, was not reared, although *Perilampus chrysopae* was well represented.

SUMMARY

In a study of the parasitic fauna of the genus *Chrysopa* in southern California a total of fifteen species of insect parasites belonging to nine families of the Hymenoptera and Coleoptera was reared from about 12,000 cocoons of *Chrysopa californica* Coq. and *C. majuscula* Banks. *Isodromus iceryae*, *Perilampus chrysopae*, and *Tetrastichus chrysopae* attack the active larval stages and emerge from the cocoons of *Chrysopa californica; Trichogramma embryophagum* parasitizes the egg, and *Chrysopoctonus patruelis*, *Gelis* sp., *Hydnocera scabra*, and *H. affiliata* the stages within the cocoon. The only primary parasites of *C. majuscula* are *Isodromus niger* and *Helorus paradoxus*, both of which attack the larvae and issue from the host cocoons. Parthenogenetic arrhenotokous reproduction occurs in all the hymenopterous species except *Hemiteles tenellus* and possibly *Gelis* sp.

The hyperparasites *Chrysopophagus compressicornis*, *Pachyneuron californicum*, and *Dibrachys cavus* were reared from the cocoons of both *Chrysopa californica* and *C. majuscula*, whereas *Arachnophaga picea* and *Hemiteles tenellus* issued only from those of *C. californica*. Both *D. cavus* and *H. tenellus* will also occasionally develop as primary parasites.

Helorus paradoxus possesses greatly enlarged peritrophic sacs which become much compressed just before pupation, apparently functioning as a filter to extract excess liquid from the meconium which is retained through the pupal stage.

The mature larvae of *Isodromus niger* and *I. iceryae* form individual cells within the distended host derm — apparently from membranous larval sheaths formed during the second instar.

When eggs of *Chrysopophagus compressicornis* are laid in mature host pupae, the parasite frequently completes its development in the abdomen of the adult host after the latter has issued from the *Chrysopa* cocoon.

Perilampus chrysopae deposits its eggs upon the leaves of plants where they hatch. The motile, planidium-type larvae attach themselves to the larvae of chrysopids. The presence of aphids, the prey of lacewings, stimulates oviposition. Larvae commence feeding only after the *Chrysopa* has spun its cocoon and pupated.

Approximately sixty-one species of insect parasites have been recorded from the Chrysopidae, the majority of which belong to the Chalcidoidea and Ichneumonoidea; the Serphoidea contains 12 chrysopid parasites, the coleopterous family Cleridae two species, and the Diptera (Chironomidae) one species. The latter is a parasite of the adult stage, five species are egg parasites, and the remainder attack either larvae or pupae, and emerge from the host cocoon.

In nature, the abundance of *Chrysopa* is largely determined by the availability of prey, whereas the degree of parasitism is predominantly a function of host density. Parasitism in general, though frequently very high, seems to have relatively little effect upon the average density of *Chrysopa* populations.

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Names of new genera and species are printed in **boldface**.